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A Revision of Helicoplacoids and Other Early Cambrian Echinoderms of North America

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A Revision of Helicoplacoids and Other Early Cambrian Echinoderms of North America

by

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This dissertation is dedicated to Mary and Frijole.

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A Revision of Helicoplacoids and Other Early Cambrian Echinoderms of North America

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The Lower Cambrian rocks of North America contain the remains of several species of echinoderms, including helicoplacoids, the eocrinoids *Gogia*, *Lepidocystis*, and *Kinzercystis*, and the edrioasteroids *Camptostroma* and *Stromatocystites*.

Camptostroma roddyi Ruedemann, 1933 is a large echinoderm from the Lower Cambrian Kinzers Formation of southeastern Pennsylvania. The animal has a unique dual-layered oral surface, and a large aboral suction pad used for attachment to skeletal debris. Thought by some authors to be ancestral to the edrioasteroids, it clearly belongs in a clade with the other early edrioasteroids.

Helicoplacoids are from the Lower Cambrian Poleta Formation and equivalent units across the western edge of North America. The group was thought to be represented by nine species; this number is reduced here to three species, with the remainder of helicoplacoid disparity accounted for by

ontogenetic variation. These triradiate spindle-shaped echinoderms were capable of expansion and contraction by means of cloacal pumping, and attached to skeletal debris or semi-lithified matgrounds by means of a suction pad. Rather than representing an ancestral triradiate form that served as the template for a "2-1-2" ambulacral arrangement, these disparate echinoderms are derived from the ancestral pentameral edrioasteroid bauplan.

Gogia is well represented in the Lower Cambrian rocks of California and Nevada by five species, four of which are new and are described here. This is now understood to be the most diverse echinoderm genus from the Early Cambrian. Members of this group attached to skeletal debris by using a suction pad, and fed by employing retractable spiraled brachioles.

Stromatocystites walcotti Schuchert, 1919 is from Lower Cambrian rocks from Bonne Bay, Newfoundland. It is a flat edrioasteroid with a retractable suctorial aboral surface devoid of a pad. This morphologic feature delineates the group from other Middle Cambrian *Stromatocystites*, warranting renaming herein.

A tree generated for these groups shows that helicoplacoids, *Gogia*, Imbricata, and the eocrinoids (*Gogia* + Imbricata) all constitute monophyletic groups, while edrioasteroids are polyphyletic. Early Cambrian echinoderms are found with only one or (rarely) two species occupying the same morphospace, a pattern repeated by Middle Cambrian groups.

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Chapter 1 - Introduction

Introduction

The Early Cambrian records the near simultaneous first appearances of many major animal groups, without obvious fossil precursors in the Precambrian rock record. This phenomenon, known as the "Cambrian Explosion," is considered to be either a real event accelerated by adaptation to fill unoccupied ecospace, or a preservational event, caused by the biomineralization and/or increase in size of small soft-bodied precursors that unlocked an evolutionary arms race. The time period, because of an adaptive landscape devoid of competitors, is characterized by novel morphologies in groups that had yet to fix characteristics considered diagnostic of the group. Most notable is the disparity and diversity shown by the Arthropoda, which has sub-groups classified as "problematica" because of a lack of familiar emergent characteristics. Early echinoderms, while not as diverse as the Arthropods, show bodyplans drastically different from later Phanerozoic and modern echinoderms.

The Ediacaran World

Simple organisms devoid of any evidence of a gut characterized the fauna of the terminal Neoproterozoic. Predation had not yet arisen, leading the time period termed the "Garden of Ediacara" to highlight the lack of interaction between members of this fauna (McMenamin, 1986, 1998). The fauna consisted of frond-like organisms, such as *Charnodiscus*, *Charnia*, and *Spriggina*, mat-like organisms, such as *Dickinsonia* and *Phylozoon*, discoidal organisms, such as *Tribrachidium* and *Arkarua* (Gehling, 1987),

and possible cnidarians, such as *Cyclomedusa*, *Ediacara*, and *Kimberella* (Bottjer, 2002). Some members of the fauna have been attributed to metazoan groups, such as the echinodermal affinities assigned to *Tribrachidium* (Glaessner and Wade, 1984) and *Arkarua* (Gehling, 1987), trilobite affinities assigned to *Spriggina* (McMenamin, 2003), and polychaete affinities assigned to *Dickinsoina* (Bottjer, 2002). It has also been proposed that the fauna is entirely composed of lichens (Retallack, 1994), and that the fauna represents the sister taxon to Eumetazoa, forming the stem-group Vendobionta (Buss and Seilacher, 1994).

The fauna disappeared at the end of the Proterozoic, with a few holdovers surviving into the Middle Cambrian (Conway Morris, 1993; Briggs et al., 1994). Ediacaran organisms, regardless their taxonomic affinities, are regarded to have been adapted for survival on microbially bound sediments. These matgrounds provided anchorage and possibly sustenance (Seilacher, 1997; Bottjer et al. 2000; Bottjer, 2002).

The Neoproterozoic-Cambrian Boundary

The end of the Proterozoic was marked by a transition from Icehouse to Greenhouse conditions brought about by supercontinental breakup (Eerola, 2001). Continents drifted from polar regions into equatorial regions (Smith, 2001), changing sea level and available shelf-space (Brasier, 1982), ocean chemistry and circulation (Cook and Shergold, 1984), which set the stage for biotic change.

These environmental changes instigated two concurrent biotic changes. The first is the "Cambrian Substrate Revolution," which is a term coined by Bottjer et al. (2000) to describe the decimation of Precambrian-style matgrounds in the Early Cambrian by

burrowing organisms. The advent of the ability to move sediment drastically changed community dynamics, forced the extinction of animals that were obligate mat-stickers, and opened new ecospace on and within the substrate. Secondly, metazoans developed predatory behavior simultaneously in several groups, which forced an evolutionary arms race between predators and prey, ultimately forcing the development and elaboration of skeletons (Vermeij, 1984) and an increase in body size (Peterson, et al. 2005). Both of these developments conspired to increase metazoan preservational potential, heralding a period of high rates of cladogenesis not seen at any other time in the history of the metazoa.

The "Cambrian Explosion"

The base of the Cambrian is marked worldwide by the diversification of trace fossils (Crimes, 1992), followed by the spread of the Tommotian "small shelly" fauna (Rozanov and Zhuravlev, 1992), which is followed by the first occurrence of trilobites, including *Repinaella* (Geyer, 1996), *Eofallotaspis*, and *Fallotaspis* (Hollingsworth, 2005). By the end of the Atdabanian, the exceptionally preserved fauna of the Chengjiang lagerstätte appeared in the record, showing tremendous amounts of biodiversity. The fauna includes many problematic arthropods, stem vertebrates, lobopods, hyoliths, priapulid worms, ctenophores, sponges, and brachiopods (Hou et al. 2004). Conspicuously absent are echinoderms, save for the questionably diagnosed fossils *Vetulicolia catenata* and *Dianchicystis jianshanensis* (Shu et al., 2004).
Later Early Cambrian lagerstätten include the Sirius Passet fauna of Greenland, notable for the occurrence of *Halkiera evangelista*, an enigmatic animal of questionable affinity,

and a diverse arthropod fauna (Conway Morris, 1998), and the Kinzers Shale of Pennsylvania, notable for a diverse arthropod and echinoderm assemblage (Stose and Stose, 1944; Campbell and Kauffman, 1969).

The Middle Cambrian saw the advent of additional lagerstätten, including the Kaili Biota of China (Zhao et al. 1994), Burgess Shale of Canada (Whittington, 1985), Spence Shale, Wheeler Formation, and Marjum Formation of Utah (Hagadorn, 2001). These faunas preserve the diverse remains of arthropods, echinoderms, basal vertebrates, sponges, brachiopods, mollusks, priapulid worms, polychaete worms, sponges, cnidarians, ctenophores, and many additional organisms of questionable affinity.

These lagerstätten are exceptional in that they preserve soft tissues not normally associated with fossil deposits. Typical deposits only preserve the hard parts of trilobites, brachiopods, and echinoderms, giving the false impression of a depauperate fauna (Briggs et al., 1994). Instead, lagerstätten show the Cambrian experienced far more diversity, including many groups common in the modern that otherwise were thought not to exist in deep time.

Early Echinoderms

Modern and ancient echinoderms share the echinoderm synapomorphies of a skeleton composed of monocrystalline, microporous, high-magnesium calcite plates, a water vascular system with tube feet, and either pentamery or some variant thereof. Aside from these common features, the ancient and modern groups have little in common with each other.

Early Cambrian echinoderms include helicoplacoids, the eocrinoids *Gogia*, *Kinzercystis*, and *Lepidocystis*, and the edrioasteroids *Camptostroma* and *"Stromatocystites" walcotti*. These groups are found exclusively in North America, except for the occurrence of an eocrinoid attributed to *Gogia* from Spain (Ubaghs and Vïzcaino, 1990), and isolated echinoderm plates from England (Donovan and Paul, 1982) and Siberia (Rozhnov et al., 1992). Each shows a widely disparate body plan, with few synapomorphies showing relationships

Prior to this study, there were nine species of helicoplacoids, one species of *Gogia*, and the edrioasteroids *Camptostroma roddyi* and *Stromatocystites walcotti*. In this report, the nine helicoplacoid species are synonymized to three, four new species of *Gogia* are named, *Camptostroma roddyi* is redescribed, and *Stromatocystites walcotti* is renamed *Schuchertidiscus walcotti* based on a new description. These groups are included in a phylogeny of Early Cambrian echinoderms, which shows that the Early Cambrian eocrinoids, *Gogia*, lepidocystids, and helicoplacoids all constitute monophyletic groups, whereas the edrioasteroids are a polyphyletic group.

These echinoderms are found attached to skeletal debris or matgrounds within the siliciclastic members of mixed carbonate-clastic sedimentary systems on the northern and southern coasts of the Early Cambrian paleocontinent Laurentia, which are now the western and eastern edges, respectively, of present-day North America. Because echinoderms are composed of small skeletal plates held together by soft tissues, they are rarely preserved, but where conditions are conducive to their preservation, they appear to be abundant, and gregarious. Most new material studied herein was brought to the attention of the author by amateur trilobite collectors who sent echinoderm material to the

University of Texas over the past two decades. A summary of locality information for new material collected or donated for this study is included in Table 1.1.

A stratigraphic range chart for Lower Cambrian echinoderm-bearing rocks shows relative ages for each unit (Figure 1.1). The oldest echinoderm fossils are incomplete thecal plates from the Lower Cambrian Campito Formation of eastern California. The oldest unequivocal echinoderms known from complete specimens are the helicoplacoids from the overlying Poleta Formation. Echinoderms become more diverse in *Bonnia-Olenellus* time, which saw the first occurrences of the edrioasteroids and *Gogia*. Helicoplacoids became extinct by the end of *Nevadella* time, leaving no apparent descendants derived from their spiraling body plan. Each of the two edrioasteroid genera became extinct, but members of the Class Edrioasteroidea diversified and survived rather successfully until the Pennsylvanian. The genus *Gogia* survived until the end of the Middle Cambrian, diversifying into a total of 14 named Early to Middle Cambrian species, and several more that have yet to be named. The Subclass Blastozoa, of which *Gogia*, *Kinzercystis*, and *Lepidocystis* are the first representatives, survived until the Permo-Triassic extinction.

Based on the new descriptions and revisions carried out here, it is apparent that Early Cambrian echinoderms were widely disparate, but show little within-group diversity. Furthermore, aside from the helicoplacoids, a single echinoderm species is found at each locality and horizon, suggesting competitive dominance of a single body plan per temporal and spatial unit. Helicoplacoids appear to have been very successful over a large spatial but short temporal scale, with the same species occurring from what is now California to British Columbia, Canada. This suggests echinoderms occurred in

environments that only rarely experienced conditions conducive to preservation of these fossils. In this regard, echinoderms show the same pattern as other taxa present during the “Cambrian Explosion,” namely great disparity but little within-group diversity.

TMM Locality #	Old Number	Age	Formation	Member	Zone
UT TMM 2029	WP1	Early Cambrian	Poleta	Lower	*Nevadella*
UT TMM 2030	WP13	Early Cambrian	Poleta	Upper	*Olenellus*
UT TMM 2031	WP10	Early Cambrian	Poleta	Upper	*Nevadella*
UT TMM 2032	WP8	Early Cambrian	Poleta	Upper	*Nevadella*
UT TMM 2033	WP9	Early Cambrian	Poleta	Upper	*Nevadella*
UT TMM 2034	WP11	Early Cambrian	Poleta	Upper	*Nevadella*
UT TMM 2035	WP7	Early Cambrian	Poleta	Upper	*Nevadella*
UT TMM 2036	WP2	Early Cambrian	Poleta	Lower	*Nevadella*
UT TMM 2037	WP3	Early Cambrian	Poleta	Lower	*Nevadella*
UT TMM 2038	WP12	Early Cambrian	Poleta	Upper	*Nevadella*
UT TMM 2039	WP14	Early Cambrian	Poleta	Upper	*Nevadella*
UT TMM 2040	IS1	Early Cambrian	Poleta	Upper	*Nevadella*
UT TMM 2041	IS2	Early Cambrian	Poleta	Upper	*Nevadella*
UT TMM 2042	AQ1	Early Cambrian	Addy Quartzite		*Nevadella*
UT TMM 2043	IP1	Early Cambrian	Carrara	Gold Ace Limestone	*Olenellus*
UT TMM 2044	IP2	Early Cambrian	Carrara	Gold Ace Limestone	*Olenellus*
UT TMM 2045	IP3	Early Cambrian	Carrara	Pyramid Shale	*Olenellus*
UT TMM 2046	SM1	Early Cambrian	Saline Valley		*Olenellus*
UT TMM 2047	PM1	Early Cambrian	Latham Shale		*Olenellus*
UT TMM 2048	LP1	Early Cambrian	Kinzers		*Olenellus*
UT TMM 2049	N/A	Early Cambrian	Carrara	N/A, 15m below FAD of *N. multinodus*	*Olenellus*
UT TMM 2050	WP15	Early Cambrian	Campito	Montenegro	*Nevadella*

Table 1.1A. Locality, Age, Formation, Member, and Zone of Lower Cambrian echinoderm-bearing rocks.

TMM Locality #	Subzone	Lat	Long	State	County
UT TMM 2029		37° 16.71'N	118° 10.17'N	CA	Inyo
UT TMM 2030	Lower *Ogygopsis*	37° 17.40'N	118° 08.42'N	CA	Inyo
UT TMM 2031		37° 16.75'N	118° 10.51'N	CA	Inyo
UT TMM 2032		37° 16.50'N	118° 09.89'W	CA	Inyo
UT TMM 2033		37° 16.14'N	118° 10.12'W	CA	Inyo
UT TMM 2034		37° 16.36'N	118° 10.17'W	CA	Inyo
UT TMM 2035		37° 17.66'N	118° 08.67'W	CA	Inyo
UT TMM 2036		37° 16.70'N	118° 09.47'W	CA	Inyo
UT TMM 2037		37° 16.73'N	118° 10.45'W	CA	Inyo
UT TMM 2038		37° 17.40'N	118° 08.48'W	CA	Inyo
UT TMM 2039		37° 16.70'N	118° 09.50'W	CA	Inyo
UT TMM 2040		37° 43.60'N	117° 19.45'W	NV	Esmeralda
UT TMM 2041		37° 43.28'N	117° 18.75'W	NV	Esmeralda
UT TMM 2042		48° 21.18'N	117° 50.47'W	WA	Stevens
UT TMM 2043		35° 53.54'N	116° 04.17'W	CA	Inyo
UT TMM 2044		35° 53.12'N	116° 03.91'W	CA	Inyo
UT TMM 2045	*Nephrolenellus multinodus*	35° 53.64'N	116° 04.62'W	CA	Inyo
UT TMM 2046		37° 42.72'N	117° 27.50'W	NV	Esmeralda
UT TMM 2047	*Bristolia*	35° 01.64'N	115° 30.04'W	CA	San Bernardino
UT TMM 2048	*Wanneria walcottana*	N/A	N/A	PA	York
UT TMM 2049		N/A	N/A	NV	Lincoln
UT TMM 2050	*Nevadia*	N/A	N/A	CA	Inyo

Table 1.1B. Subzone, Latitute and Longitude, State, and County for Lower Cambrian echinoderm-bearing rocks.

TMM Locality #	Area	Fauna
UT TMM 2029	Westgard Pass	Echinoderm debris
UT TMM 2030	Westgard Pass	*Ogygopsis* trilobites
UT TMM 2031	Westgard Pass	*Helicoplacus, Nevadella*
UT TMM 2032	Westgard Pass	*Helicoplacus, Nevadella*
UT TMM 2033	Westgard Pass	*Helicoplacus, Nevadella*
UT TMM 2034	Westgard Pass	*Helicoplacus, Nevadella*
UT TMM 2035	Westgard Pass	*Helicoplacus, Nevadella*
UT TMM 2036	Westgard Pass	Echinoderm debris
UT TMM 2037	Westgard Pass	Echinoderm debris
UT TMM 2038	Westgard Pass	*Olenellus* trilobites, *Gogia*
UT TMM 2039	Westgard Pass	*Helicoplacus*
UT TMM 2040	Indian Springs	*Helicoplacus, Nevadella*
UT TMM 2041	Indian Springs	*Helicoplacus, Nevadella*
UT TMM 2042	Addy	Helicoplacoid debris, *Nevadella addyensis*
UT TMM 2043	Immigrant Pass	*Gogia inyoensis*, *Olenellus gilberti*
UT TMM 2044	Immigrant Pass	*Gogia inyoensis*, *Olenellus gilberti*
UT TMM 2045	Immigrant Pass	*Gogia lockeri*, *Nephrolenellus multinodus*
UT TMM 2046	Split Mountain	*Gogia mccollumi*
UT TMM 2047	Providence Mts.	*Gogia fowleri*
UT TMM 2048	York	*Camptostroma roddyi, Olenellus getzi*
UT TMM 2049	Groom Range	*Olenellus gilberti, O. clarki, O. nevadensis Naryella*
UT TMM 2050	Westgard Pass	*Nevadia*

Table 1.1C. Geographical area and associated fauna of Lower Cambrian echinoderm-bearing rocks.

TMM Locality #	Notes	Collector(s)
UT TMM 2029	Eocrinoid or edrioasteroid debris	BCW, JS, CS, JBM, NAS, LL
UT TMM 2030	Trilobite pygidia	BCW, JBM
UT TMM 2031	N. B. McCulloch quarry	BCW, JS, CS, JBM, NAS, JCW, SCW, LL
UT TMM 2032		BCW, JBM
UT TMM 2033		BCW, JBM
UT TMM 2034		BCW, JBM
UT TMM 2035		BCW, JS, CS, JBM
UT TMM 2036	Eocrinoid or edrioasteroid debris	BCW, JS, CS, JBM, NAS
UT TMM 2037	Eocrinoid or edrioasteroid debris	BCW, JS, CS
UT TMM 2038	Incomplete *Gogia*	BCW, JBM, PG
UT TMM 2039	Incomplete *Helicoplacus nelsoni*	BCW, JCW
UT TMM 2040		BCW, JS, JBM, JCW, SCW
UT TMM 2041		BCW, JS, JBM, JCW, SCW
UT TMM 2042	Per. To collect granted by Cal Davis, 07-10-03	BCW, JBM
UT TMM 2043	Locality of Folwer specimen	EF
UT TMM 2044	Locality adjacent to fire pit	BCW, MW, JBM
UT TMM 2045	*Anomalocaris* claw, *Olenellus gilberti*	BCW, MW, JBM, CL
UT TMM 2046	Phyllitic shale	LM, MM
UT TMM 2047		EF
UT TMM 2048		JC, PK
UT TMM 2049	Contemporary of Gold Ace LS	LM, MM
UT TMM 2050	Incomplete echinoderm plates	EF

JC = John Collidge III
EF = Ed Fowler
PG = Peter Guth
PK = Peter Kohler
CL = Carl Locker
LL = Lindsey Leighton
LM = Linda McCollum
MM = Michael McCollum
JBM = James B. McGuire
CS = Christie Schneider
NAS = Nathan A. Simmons
JS = James Sprinkle
BCW = Bryan C. Wilbur
MW = Meng-Chieh Wilbur
JCW = Jay C. Wilbur
SCW = Scott C. Wilbur

Table 1.1D. Notes and collector information for Lower Cambrian echinoderm-bearing rocks.

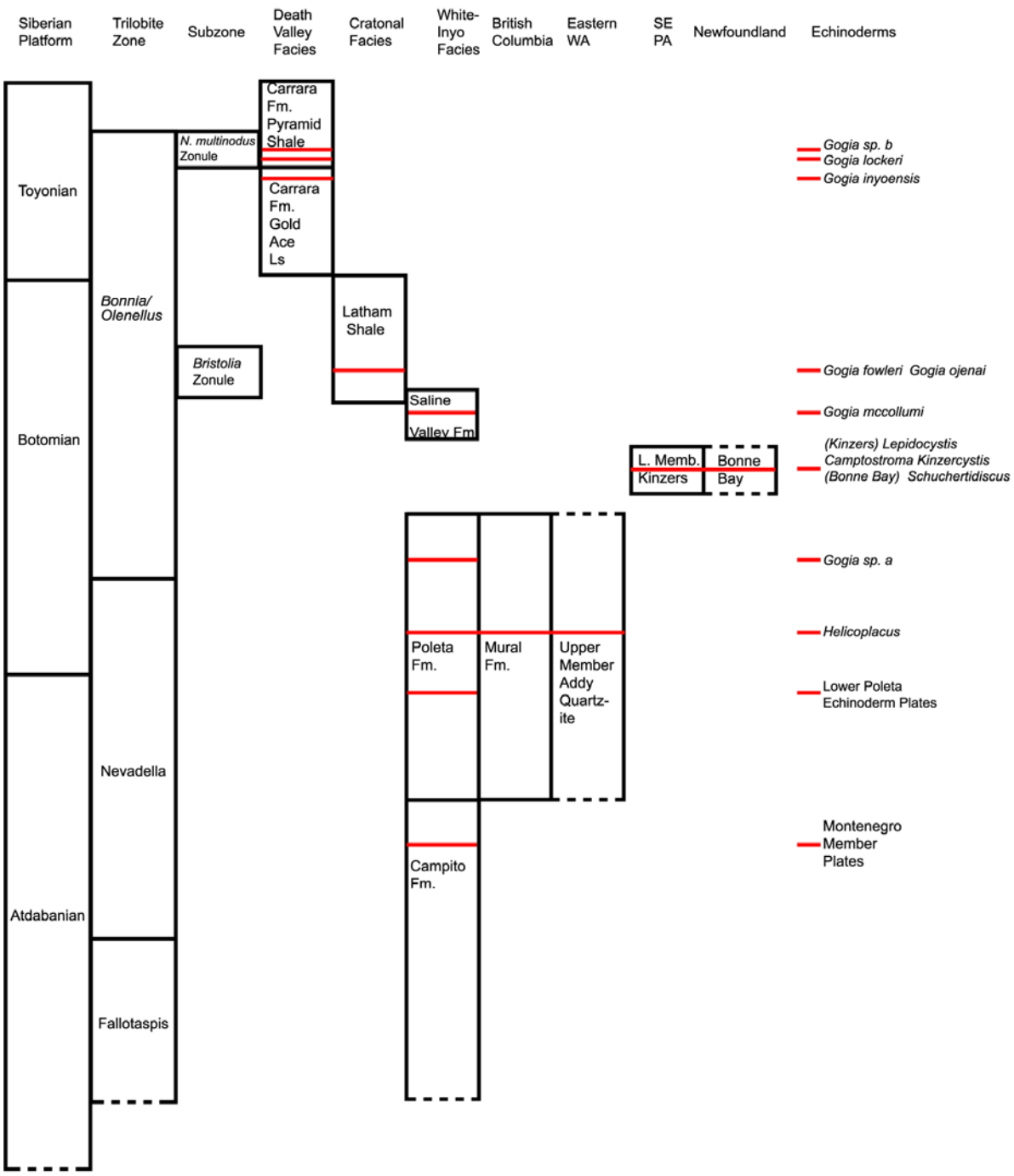


Figure 1.1 Lower Cambrian correlation chart for echinoderm bearing rocks (Schuchert and Dunbar, 1934; Lochman-Balk and Wilson, 1958; Campbell and Kauffman, 1969; Stewart, 1970; Fritz and Mountjoy, 1975; Nelson, 1976; Palmer and Halley, 1979; Spizharskiy et al. 1984; Miller, 1996; Zhuravlev and Riding, 2000; Alison R. Palmer, personal communication; Mark Webster, personal communication)

Chapter 2 – *Camptostroma Roddyi* Ruedemann, 1933

Introduction

Camptostroma roddyi is a large domal echinoderm from the *Bonnia-Olenellus* Zone of the lower member of the Lower Cambrian Kinzers Formation of York and Lancaster, Pennsylvania. The animal has suffered many misinterpretations, having been originally described as a floating scleritized hydrozoan (Ruedemann, 1933), and an inverted floating echinoderm (Durham, 1966, 1968a).

Revisions carried out by Derstler (1981, 1985) and Paul and Smith (1984) for the most part concur on general morphological features, but disagree on overall shape. Derstler reconstructed the animal with a large domal oral surface and a reduced aboral surface, while Paul and Smith (1984) reconstructed the animal with a reduced oral surface and a large inverted conical aboral surface, which it supposedly used as an anchor in soft substrates in a manner similar to that argued for in helicoplacoids (Durham and Caster, 1963, 1966; Durham 1967a, 1993) and *Lepidocystis wanneri* (Durham, 1967c).

The oral surface is composed of five ambulacra in a "2-1-2" arrangement (Sprinkle, 1973), with the mouth medial. Each ambulacrum is composed of biserial floor plates and multi-element cover plate sheets. Between the ambulacra are five epispire-bearing interrays. An anal pyramid occurs in the CD interray near the edge of the oral surface. The theca is enclosed by epispire-bearing plates on the oral surface, imperforate multi-sized plates that are arranged into pleats on the aboral surface, and an aboral flexible pad that the animal used to attach by suction to hard or semi-lithified substrates (Guensburg and Sprinkle, 2001; Wilbur, 2004). *Camptostroma* had an upward-oriented

domal oral area, which elevated the ambulacra some distance above the sediment-water interface. Food was collected by tube feet, which then transported the food particles to the mouth along the base of the ambulacrum.

Materials and Methods

Camptostroma specimens are preserved most frequently as natural molds in the fissile siltstones and mudstones of the lower member of the Lower Cambrian Kinzers Formation of York and Lancaster Counties, southeastern Pennsylvania (Figure 2.1). Durham (1966) reported original calcite plate material preserved in a single specimen, but the author did not encounter this specimen, or any others like it in the collections at either the United States National Museum (USNM), Washington, D. C., or the North Museum (NM), Franklin and Marshall College, Lancaster, Pennsylvania, suggesting this type of preservation is exceedingly rare. Latex casts are made of the natural molds in order to study the anatomical features of these echinoderms. The material housed at the USNM is preserved in a well-indurated mudstone from outcrop in the Lancaster area, while the material housed at the NM and the Texas Memorial Museum (TMM), Austin, Texas, is from a locality in the York area characterized by friable siltstones. This makes latex cast making more difficult, as great care must be taken in removing dried latex from the rock in order to not remove any matrix. Application of water to the edge of the well-dried cast before peeling minimizes damage to the fossils.

Making latex casts required that the natural molds were first cleaned and wetted, then filled with a solution of "Mold Builder" liquid latex rubber, manufactured by Environmental Technology Incorporated of Fields Landing, California, colored with

black powder tempera, manufactured by Palmer Show Card Paint Company of Troy, Michigan. The mixture usually stains the rock upon which it is applied, but the process is otherwise non-destructive. Museum specimens studied herein were cast using uncolored latex in order to avoid the previously mentioned stains. The latex casts were darkened in the laboratory by painting them with waterproof black India ink, manufactured by Faber-Castell Corporation, of Newark, New Jersey. The resulting smoked casts show nearly the same quality of fine details as the blackened latex casts. The one failing of this method occurs if ink is too liberally applied, resulting in cracks in the fine layer of ink upon drying of the coat.

After drying, which takes on average three days depending on the thickness of latex applied and ambient humidity, the latex is slowly peeled away, resulting in a blackened latex positive of the moldic fossil. These are then "smoked" with ammonium chloride sublimate that whitens the higher relief of the fossils, leaving the crevasses darkened. The ammonium chloride sublimate is applied with a long glass tube with a spherical cavity on one end and a rubber atomizer bulb with a one-way valve on the other. Ammonium chloride is inserted into the spherical cavity and warmed above a burner. Contracting the bulb wafts air over the sublimating ammonium chloride, which carries it to the surface of the cast. The ammonium chloride used in this study was manufactured by Matheson, Coleman and Bell, of Northwood Ohio, Los Angeles, California, and East Rutherford, New Jersey.

Specimens Studied

Specimens of *Camptostroma* from the NM, and the USNM were studied in the preparation of this manuscript. Additional specimens collected by amateur collectors John Coolidge III and Peter Kohler, both of Lancaster, Pennsylvania, were donated to the TMM. A few specimens from the personal collection of John Coolidge III were cast at his home; the latex casts of these specimens were placed in the TMM Collections.

Previous Work

Rudolph Ruedemann originally described *Camptostroma roddyi* (Ruedemann, 1933) as a spicule-bearing colonial hydrozoan (Coelenterata) (Figure 2.2). The holotype of this species (USNM 85181) is a part-counterpart pair, one side of which preserves what were interpreted as the bell, lappets, and a tentacle of a hydrozoan (2.3). The fossil retains two readily apparent morphologically different regions separated by a deep furrow. The first is a large disc composed of a meshwork of spicules surrounding dimples; the second is a series of pleated sheets composed of small multi-sized spicules, the original composition of which was hypothesized to be either carbonate or chitin, although it was acknowledged that hydrozoans do not mineralize because of the negative buoyancy of these materials. Ruedemann conceded that the multiplated morphology was suggestive of an echinoderm, but he did not recognize any trace of a mouth or anal pyramid, two structures commonly found in other fossil echinoderms. The plating also appeared too different from known edrioasteroids and eocrinoids to conclude echinodermal affinity. Aside from echinoderms, Ruedemann mentioned but discounted poriferan, receptaculitid, and stromatoporoid affinities.

Resser and Howell (1938) included *Camptostroma roddyi* in a survey on the fauna of the Early Cambrian *Olenellus* Zone of the Appalachians, along with the non-echinoderm *Camptostroma resseri*, a fossil that does not bear spicules, shows no echinoderm characters, is not from the same stratigraphic interval, and was collected at a locality in Washington County, New York. No new systematic or morphologic insight was added by this work.

Keislinger (1939) interpreted *Camptostroma roddyi* as a medusoid coelenterate, placing it in class Scyphozoa, order Coronata, family Atollidae. The family was diagnosed by having either four bodily divisions with eight sense organs per division or four divisions with sixteen sense organs per division; the latter diagnosis was considered descriptive of *Camptostroma*. Kieslinger's interpretation was affirmed in *The Treatise on Invertebrate Paleontology* by Harrington and Moore (1956), who agreed that the body was composed of gelatinous material which shrank upon stranding, resulting in the apparent rugosity of the holotype. It was placed in class Scyphozoa, order Coronatida, family Collaspididae. The Coronatida are diagnosed by a dome-shaped to conical bell that is fringed by 4 to 32 pedalia, or fleshy lappets, which bear either sense organs or tentacles at the terminus. Family Collaspidae is diagnosed by the possession of more than eight sense organs and more than eight tentacles. This diagnosis of the "bell" (aboral surface) of the holotype was made despite the presence of skeletal ossicles, a fact that may have been overlooked as the skeleton of the holotype was leached of its skeletal material before collection.

Camptostroma roddyi was placed in Echinodermata by Durham (1966). Fieldwork by Durham resulted in several new specimens, one of which that retained

calcite plates with stereom, which is a synapomorphy of Echinodermata. The disc-shaped structure diagnosed by Ruedemann as the "bell" was thought by Durham to represent the oral surface of the echinoderm, with a central mouth. The same structure in an adjacent specimen showing an interior view was considered to represent the aboral surface, with a central anal pyramid marked by vertical lath-shaped plates. Durham noticed that the surface was made up of lenticular plates surrounded by much smaller secondary plates that were visible only in this relaxed specimen; when constricted, the smaller plates "buried" the larger lenticular plates. Between these supposed oral and aboral surfaces were a series of ridges and grooves toward the aboral surface, which graded into small triradiate ossicles surrounding large plates with notched edges toward the oral surface. These plates were not tightly sutured, and were recognized as being similar to notched plates in some eocrinoids (Durham, 1966).

Durham, like Ruedemann, did not recognize the true anal pyramid present upon one of the type specimens or the ambulacral areas indicating an oral surface; instead the interior and exterior lower surfaces of two adjacent specimens were interpreted as the oral and aboral surfaces of a single specimen splayed out on a single bedding plane. *Camptostroma* was therefore inferred to have the same orientation as the supposed cnidarian it was originally understood to be, with a downward-facing oral surface and an upward facing aboral surface with an anal pyramid. Durham argued that this orientation was suggestive of medusoid lifestyle, and that *Camptostroma* was probably bathypelagic or planktonic. The mouth on the oral surface was interpreted to be a raised multiplated area without ambulacral areas leading to it. The ambulacra that were present were interpreted as situated along tentacles inserted at the edges of the oral surfaces, which

carried food particles to the edge of the oral disc, where a "ciliary mechanism" delivered the food to the mouth. No pentamerism was recognized in this unconventionally understood echinoderm; considering the interpretation of convergence on a medusoid shape, it followed that the animal was interpreted as radially symmetrical (Durham, 1966).

Durham did not make a definitive diagnosis at to which higher taxon within Echinodermata *Camptostroma* belonged to, but he did suggest the triradiate plating was suggestive of holothurians, the skeletal plates of which are not known until the Ordovician (Sprinkle, 1980; Sprinkle and Guensburg, 2004). Furthermore, the wayward ambulacrum appeared to be part of the peripheral water vascular system of holothurians rather than part of the oral system. However, plated peripheral ambulacral appear only in the Devonian holothurian *Paleocucumaria*, and for this reason Durham placed *Camptostroma* in the monotypic Class Camptostromatoidea in a brief statement at the end of his short article.

These sentiments were repeated by Durham (1968a) in a revision to the previous discussion of *Camptostroma* in the Treatise on Invertebrate Paleontology, which properly places the group in Echinodermata, rather than Coelenterata. He asserted that the oral surface of *Camptostroma* lacked epispires and ambulacra leading to a central mouth, and that it was a free-living medusiform echinoderm. Other morphological characters were misdiagnosed, including the mouth, anal pyramid, and arms.

Bell (1980) wrote a short paper for the Paleontological Society on the topic of edrioasteroid systematics. There, Bell included *Camptostroma* in the new order Stromatocystitida, in class Edrioasteroidea. Homologies for the group were a subgloboid

theca, which was circular to pentagonal in plan view; an oral frame consisting of enlarged proximal ambulacral floor plates; hydropore near right posterior margin of oral area; ambulacra composed of biserial floor plates with sutural pores and irregular biseries of cover plates; and polygonal interambulacra with sutural pores (Bell, 1980). Also included in the group were the Early to Middle Cambrian *Stromatocystites* and Middle Cambrian *Walcottidiscus*. No known specimens of *Camptostroma* show the oral frame, and *Walcottidiscus* (Bassler, 1935, 1936; Smith, 1985) shows no evidence of sutural pores in the interambulacral areas or anywhere else on the theca for that matter, calling into question the validity of the group, which was likely erected to include three of the earliest and most generalized taxa. Despite the questionable ordinal assignment and diagnosis, this paper marked the first inclusion of *Camptostroma* within Class Edrioasteroidea. Furthermore, this work suggested that *Camptostroma* was more or less a generalized edrioasteroid, with an oral-surface-upward orientation, and a sessile epifaunal lifestyle, points that contradicted the radical interpretation of Durham.

Camptostroma was investigated by Derstler (1981, 1985) as part of a survey of the echinoderms of the Early Cambrian. It was in the 1981 work that *Camptostroma* was first recognized as a basal edrioasteroid. Important diagnostic characters following the work of Bell (1980) included multiplated ambulacral cover plate sheets, aboral epispires, and the lack of a calcified oral ring. Derstler was also the first to identify anatomical features hinted at by Bell (1980) but not discussed specifically in *Camptostroma*, including the anal pyramid in an interray (probably CD), pentameral body plan, an oral-surface-upward orientation, and an epifaunal lifestyle (Figure 2.4). One of the two separate structures Durham (1966, 1968a) described as the mouth, Derstler redescribed as

the anal pyramid; what Durham described as free arms (Durham, 1968a), Derstler recognized as recumbent ambulacra. A reconstruction of the animal showed a domed oral surface grading into a pleated distal skirt, which articulated with the lower pad. Derstler argued (1985) that the ambulacral areas were composed of biserial floor plates with pores between sequential plates, and many layers of cover plates forming a sheet, with secondary perpendicular grooves on the interior of the sheet away from the main groove. These he proposed were an early plastic characters that eventually led to the development of brachioles in the blastozoan echinoderms.

Paul and Smith (1984) completed the most recent investigation into *Camptostroma*, studying the type specimens and new specimens accessioned to the USNM by Durham and Derstler (Figure 2.5). The surface was recognized as being divided into two distinct regions, ventral (oral) and dorsal (aboral), with the dorsal surface conical and coming to a distal terminus, presumably for insertion into soft substrates as in the interpretations of the helicoplacoids (Durham and Caster, 1963, 1966; Durham, 1967, 1993) and lepidocystids (Durham, 1968b). Ambulacra were described as being arranged in the 2-1-2 pattern described by Sprinkle (1973), with ambulacra A, B, C, and E curving clockwise at the edge of the oral surface, and D curving counterclockwise (according to the Carpenter System of ambulacral notation [Carpenter, 1884]). Interambulacral areas have large "stellate" (epispire-bearing) plates, with smaller plates between the adjoining epispires of adjacent larger plates. Interambulacral areas as well as the plating of the aboral surface were not firmly sutured in life. The notable difference in plating between the oral and aboral surfaces is the lack of epispires and the development of pleats adjacent to the edge of the oral surface. Paul and Smith (1984)

argued that an oval pore near the mouth between ossicles of the oral surface that did not bear epispires was considered the gonopore or hydropore.

Most notably, this reconstruction ignored the structure originally described as the "bell" of the animal by Ruedemann, and reconstructed by Derstler (1981) as the lower surface. Paul and Smith (1984) like Derstler (1981) did not find evidence of a peripheral rim, delineating the oral from aboral surface, but unlike Derstler, they ignored the deep furrow between the pleated sheets of plates and the "bell" (Ruedemann, 1933). This flattened disc was reconstructed as an inverted conical rooting structure for insertion into soft substrates, which was altered in appearance by taphonomic processes (Paul and Smith, 1984).

Guensburg and Sprinkle (2001) conducted a brief survey of some Early Paleozoic edrioasteroids wherein the taxonomic placement of *Camptostroma* was reviewed, which necessitated some short notes on morphology. Specifically, they were the first to recognize the aboral pad as a structure used for attachment by suction. Furthermore, they agreed with the assertion by Bell (1980) and Derstler (1981) that *Camptostroma* is an edrioasteroid.

Occurrences

Camptostroma is found in the Lower Cambrian Kinzers Formation in York and Lancaster Counties southeastern Pennsylvania (Figure 2.1). The formation is separated into three members. The lower member is composed of a basal argillaceous dolomite and dolomitic limestone (Taylor and Durika, 1990), overlain by dark calcareous shale, which grades to a phyllite toward the west. The metamorphic fabric obliterated any fossils that

may have existed (Stose and Stose, 1944). This is in turn overlain by an upper limestone interval (Resser and Howell, 1938). The rocks are interpreted as deep-water off-shelf deposits, the carbonates being deposited by debris flows from the shelf above during periods of active carbonate deposition (Taylor and Durika, 1990). The thickness of this member varies from 13 m (42 feet) to 46 m (150 feet) (Stose and Stose, 1944). The siliciclastic beds of this formation are highly fossiliferous, preserving the remains of a diverse fauna. Most notable are the arthropods *Anomalocaris pennsylvanica* (Resser, 1929; Briggs, 1979), *Roddyia typa, Tuzoia* (Resser, 1929), *Serracaris lineata* (Briggs, 1978), *Sidneyia*, Isoxys (Resser and Howell, 1938) and a diverse trilobite assemblage, most common of which are *Wanneria walcottana, Bonnia,* and *Olenellus thompsoni* (Campbell and Kauffman, 1969), some of which show soft appendages (Dunbar, 1925). Further faunal elements include *Marpolia*, *Paternia*, *Nisusia*, *Salterella* (Resser and Howell, 1938), *Hyolithes* (Campbell and Kauffman, 1969), sponges (Rigby, 1987), the enigmatic worm *Kinzeria crinita* (Capdevila and Morris, 1999), and the additional echinoderms *Kinzercystis durhami* and *Lepidocystis wanneri* (Resser and Howell, 1938; Durham, 1968b; Sprinkle, 1973).

The most prolific fossiliferous localities were found in the Lancaster area, and despite Stose and Stose's (1944) argument that this member is unfossiliferous in the York area, an outcrop immediately north of this area and another immediately northwest of York in the Shiloh area have yielded *Camptostroma* and lepidocystid fossils (Stose and Stose, 1944; Sprinkle, 1973). Charles D. Walcott, Charles Schuchert, and Atreus Wanner were the first to collect the lower Kinzers in the York area (Stose and Stose, 1944), but the trio did not collect any specimens of *Camptostroma*. The member is in places highly

deformed by metamorphic processes, distorting some trilobites to the point at which a single species was diagnosed as 14 others before these were all synonymized (Campbell and Kauffman, 1969).

Collection of the Kinzers is now difficult, as most localities have been paved over for the building of strip-malls (Sprinkle, 1973; Hagadorn, 2001), a plumbing store, and a Toys-R-Us parking lot (John Coolidge, personal communication). The educational quarry owned and managed by Franklin and Marshall College has been eroded to the point that it is unsafe, and has therefore been closed. The new material studied for this report was donated to the TMM by John Coolidge III of Lancaster, PA to the N, and the TMM, after having been removed by him and Peter Kohler from construction sites within the York-Lancaster area.

The middle member is predominantly carbonate, with argillaceous limestone enclosing white crystalline masses of limestone, known locally as "leopard rock" (Stose and Stose, 1944). These beds are interpreted as off-shelf debris flows from the shelf break above, which by the time of deposition had returned to active carbonate production. The thickness varies from 23 m (76 feet) in the Lancaster Area to 305 m (1000 feet) in the York area (Taylor and Durika, 1990). The fauna in these rocks includes archaeocyaths (Stose and Stose, 1944), and the trilobites *Bonnia capito* and *Olenellus thompsoni*, placing the rocks within the *Bonnia-Olenellus* zone, but the member does not preserve the remains of any echinoderms (Campbell and Kauffman, 1969). The upper member is characterized as a sandstone unit by Stose and Stose (1944), but Taylor and Durika (1990) characterized it as an impure carbonate unit with fine-grained siliciclastic input, suggesting either a deepening event in an off-shelf environment, or a decline in

carbonate production. This member contains a diverse fauna, which includes *Pagetia*, *Olenoides serratus*, and *Ogygopsis klotzi*, placing this horizon well within the Middle Cambrian, and coeval with the Burgess Shale, with which it share some faunal elements. This member however does not contain any echinoderm fossils (Campbell, 1971).

Morphology

The system of skeletal homology recognized by Mooi and David (1997, 1998) provides a framework for discussing the morphology of *Camptostroma*, along with other early echinoderms. The Extraxial-Axial Theory (EAT) draws comparisons of developmental and functional regions across the spectrum of the echinoderm bauplan to characterize homology. The skeleton is delineated into three separate skeletal regions, the axial, perforate extraxial, and imperforate extraxial. The axial region is the portion of the skeleton dedicated to support of the hydrovascular system. The perforate extraxial region is involved in coelom enclosure, and is "perforated" by sutural pores, which likely allowed for respiration, and other openings, including the anus and gonopore. The imperforate extraxial region is dedicated to coelom enclosure, but lacks respiratory and other body openings. In modern crinoids and in many early groups (Mooi and David, 1997, 1998; Peterson et al., 2000), this skeletal region is dedicated to stem and holdfast structures, or to other substrate interactions.

Axial Region

The axial region is the skeletal system associated with the water vascular system. This includes the ambulacral areas and mouth (Mooi and David, 1997), which are known

primarily from two well-preserved type specimens. Ambulacra are composed of three series of irregular polygonal cover plates, and a series of biserially arranged floor plates. The proximal, or primary cover plates are large, roughly hexagonal, and abut floor plates in a 1:1 ratio. Above these plates lie two secondary cover plates per primary plate, one directly above the primary, and another in the notch between primary cover plates. A row of irregular tertiary plates lies above these, with two tertiary plates per secondary. Above these lie a final quaternary plate row, which occluded with those of the opposite cover plate sheet when closed (Figures 2.6, 2.7).

The ambulacral groove is floored by biserially arranged plates elongate in the direction perpendicular to the groove and short parallel to it, with pores for ampullary compensation sacs occurring in the margins between laterally adjacent floor plates. Each floor plate is roughly "I" shaped in cross section; when aligned, the gaps between plates provided compensation space for the ampullae that connected the tube feet to the radial water vessel (Figure 2.8). Very few of the type or newly studied specimens show the interior of the ambulacrum. Paul and Smith (1984) wrote that Derstler (1981) mentions the presence of pores between laterally adjacent floor plates, but no mention can be found by the author in Derstler's work, suggesting that the reference may have been a personal communication, as this does appear in his 1985 dissertation. There, Derstler reconstructed an ambulacrum based on well-documented floor plates of *Lepidocystis* and cover plates of *Camptostroma*. The plates are elongate parallel to the ambulacrum, and short perpendicular to it, which is opposite the situation seen in the types. In no place does he figure specimens that show biserially arranged floor plates in *Camptostroma*, nor does he explicitly state that the reconstruction is based on *Camptostroma* specimens.

Cover plate sheets were opened by expansion of the ampullae at the bases of the tube feet. Paul and Smith (1984) suggested that the tube feet were attached to and served exclusively to open the cover plates, which ultimately left no structures dedicated to feeding. It is more likely that tube feet were employed in the collection of food particles, and the ampullae opened the cover plates. The ambulacrum was floored by the radial water vessel, which branched biserially to ampullae that served to distend the tube feet and open the ambulacral cover plates. The floor plates are biserial to accommodate the biserial nature of the radial water vessel.

The floor plates lie adjacent and attached to epispire-bearing interambulacral plates (Figure 2.8). Floor plates are raised in relief relative to the theca, such that the base of the floor plates abut the interambulacral plates, so that the remainder of the floor plate stands out in relief, elevating the ambulacrum above the oral surface. Ambulacra are set into and compose part of the body wall, rather than lying on top of it or having no connection to is as supposed by Durham (1966, 1968a).

A single specimen with a well-preserved oral surface shows the layout of the oral surface, despite missing a small sliver of rock from a repaired break (Figure 2.9). Ambulacra A, B, D, and E curve counterclockwise away from the mouth, and ambulacrum C curves clockwise, counter to the interpretation written by Paul and Smith (1984). Therein, Paul and Smith wrote that A, B, C, and E curved clockwise, and D curved counterclockwise, despite figuring a reconstruction with the ambulacral assignments and orientations presented here.

The mouth is incomplete because of the missing rock, but shows the typical 2-1-2 ambulacral arrangement, and opened cover plates directly over the mouth. This agrees

with the assertions of Derstler (1981) and Guensburg and Sprinkle (1994) that the mouth frame was unfused. A remnant of the anal pyramid lies in the CD interray, within the inner curve of the C ambulacrum.

The type specimen (Figure 2.3) shows a partial oral surface, but is wrinkled in many places, making for the false appearance of extra ambulacral areas. Two broad curves at the edge of the CD interray are not ambulacra at all, but wrinkles of the oral surface. One of these wrinkles is adjacent to the D ambulacrum, indicating that the wrinkle is not an ambulacrum at all ("tentacle" in Figure 2.3). The trace of the clockwise curved C ambulacrum lies on the opposite side of the interray, near another large wrinkle, indicating that the interray assignment is correct.

Perforate Extraxial Region

The perforate extraxial region is the portion of the skeleton dedicated to coelom enclosure that is perforated by epispires, or by other skeletally bound orifices. In *Camptostroma*, this includes the interrays, hydropore, and anal pyramid (David and Mooi, 1997, 1998).

Paul and Smith (1984) wrote that the oral surface was "probably gently domed" in life, and reconstructed the animal with a moderately arched oral surface (Figure 2.5), while Derstler (1981) reconstructed the animal with a hemispherical oral surface (Figure 2.4). The surface was highly flexible, and probably domed somewhere between these endpoints. The best evidence for its vaulted nature is taphonomic wrinkling of the surface. Many specimens show raised wrinkles on the oral and or aboral surfaces. Upon closer inspection, it is apparent that these are ridges that formed as oral dome was

laterally compressed, rupturing the connections between adjacent interray plates, and exposing the epispire grooves along the edges of these plates. Because of this taphonomic process, *Camptostroma* oral surfaces are typically a field of ridges and valleys.

The oral surface of Camptostroma is unique among echinoderms in that it is composed of two layers, a superior (external) layer made of typical epispire-bearing stellate plates, with additional lath-shaped and triradiate epispire cover plates, and an inferior (internal) layer composed of a cobblestone-pavement of ovate plates surrounded by lath shaped plates.

The superior surface is composed of five triangular interambulacral fields of large ornamented epispire-bearing plates (Figure 2.10) (stellate pales of Durham, 1966, 1968a) abutting the imperforate extraxial region. These plates grow as large as 2 mm in diameter, with as many as 22 epispires per plate, but typically vary between 10-20 epispires, depending on the size of the plate (Figure 2.10). The stellate plates are larger toward the mouth and smaller toward the edges of the oral area, becoming almost multi-sized at the edge of the oral surface. In the junctions between large plates are small lath-shaped and triradiate-shaped plates positioned directly over epispires, acting as covers (Figure 2.11). The only other Early Cambrian taxa that show these structures are *Gogia (Alanisicystis) andalusiae* Ubaghs and Vizcaïno 1990, and a possible undescribed incomplete eocrinoid from the Early Cambrian Carrara Formation of southeastern California. Plates adjacent to the ambulacral floor plates have less well-developed epispires, and lack epispire cover plates.

The inferior surface is composed of a cobble-stone-like pavement of ovate plates upon which the large tessellate plates of the superior surface lie (Figure 2.12). The largest ovate plates are the same diameter (approximately 2 mm) as the largest epispire-bearing plates, which follows as each inferior ovate plate supports a superior epispire-bearing plate. Several specimens that show this layer immediately below a sheet of superior plates that have in places been excavated by taphonomic processes, revealing the inferior layer. Flanking the cobbles are lath-shaped plates, many of which have a conspicuous groove down the middle of each plate, oriented away from the cobble-like plates. Each of these inferior flanking plates corresponds to a superior epispire cover plate.

The grooves in each of these lower series of flanking plates supported soft tissues that when contracted, elevated the epispire cover plates, allowing for passage of respiratory tissues. When retracted, the epispire covers dropped into position between epispires, protecting the respiratory tissues below from predators. It is clear that these two layers are distinct, and that the cobblestone pavement is not the underside of the sheet of epispire-bearing plates. It originally appeared to the author that the oral surface was folded over onto itself in a specimen that was rolled over from an upright position, which could explain the apposed external surface (ornamented epispire-bearing plates), and the internal surface with the same layer of plates. However, several specimens that are unequivocally preserved upright in part and counterpart still show both layers. These specimens show a centered lower surface, with aboral pad central, flanked by pleats. These specimens are then not folded over onto themselves, and would therefore not show the internal and external faces of the external sheets of plates. Since there is clear

evidence of two types of plates in the same upright specimens, it is clear that there are two layers of interambulacral plates. Furthermore, the few examples of stellate plates preserved upside-down show epispires along the edges, rather than the hemispherical profile that would be expected if there only one sheet of interambulacral plates.

Two different structures, ringed by radially concentric lath shaped plates and representing the anus and hydropore, are located on the oral surface. The anus, protected by radial plating typical of an anal pyramid, is located near the transition of the oral to aboral surfaces on two separate partial specimens that show no ambulacra (Figure 2.13). A single specimen shows a poorly preserved anal pyramid near the edge of the CD interray (Figure 2.10). One of these pyramids preserved in a partial specimen lacking ambulacra is in an interray wide enough to be the CD interray. The hydropore is situated immediately adjacent to the mouth, away from the midline toward the C ambulacrum. The orifice and its surrounding lath-shaped plates are flush with the surrounding stellate plates (Figure 2.14). This structure is located in a position consistent with other edrioasteroids (Resser, 1935, 1936; Bell, 1976; Derstler, 1981; Paul and Smith, 1984; Smith, 1985), but is unique in its being fringed by lath-shaped plates. The hydropore is typically a pore groove between oral frame plates, but considering the lack of a calcified oral ring, plating similar to the anus supported the structure.

Imperforate Extraxial

The imperforate extraxial region is the portion of the skeletal system lacking pores and dedicated to coelom enclosure. This skeletal region is involved in substrate interaction in ancient echinoderms as well as in modern crinoids, the only extant group

that retains it. In *Camptostroma*, the imperforate extraxial region is divided into two subregions, a central aboral flexible pad and a peripheral pleated skirt that abuts the oral surface. In the type specimen, the aboral pad is 4.0 mm in diameter; it varies from 0.6 mm to 4.0 mm in other specimens. The pleated body wall extends from the edge of the aboral pad to the oral surface with pleats oriented radially like wheel spokes. This region is 0.6 mm wide in the type specimen, and from 0.6 to 2.0 mm in other specimens. The great variability in size of these structures suggests flexibility, and ability to change shape and surface area.

The exterior of the aboral pad in the relaxed state (Figure 2.15) shows imbricate plating of two distinct regions. Larger (1-2 mm diameter) plates are surrounded by smaller adjacent plates, which overlapped when contracted. External views of contracted specimens (Figure 2.3, "bell" in Ruedemann's nomenclature) show dimpling of the pad; the dimples are the medial portions of these large plates, and the raised areas surrounding the dimples are the smaller plates stacked on top of each other. The center of the pad is composed exclusively of smaller imbricate plates, which are perpendicular to the plane of the pad. The presence of these smaller plates is either to confer greater flexibility to the center of the pad, which is crucial for initiating a seal, or because the central portion of the pad represents a growth zone. Plates increase in size toward the edges of the pad, suggesting that plate insertion occurred at the center, and growth commenced as the plates were pushed toward the edge of the pad by newly inserted elements behind them. It is likely that the central small imbricate plates carried out both of these functions. These central small imbricate plates were originally mistaken for the mouth in one internal view, and for the anal pyramid in an external view (Figure 2.14) (Durham, 1966,

1967). The function of the pad is confirmed by the fact that these overlapping imbricate plates were set in a matrix of mutable collagenous tissues. *Camptostroma* rested upon this pad on top of hard or semi-lithified substrates, then raised the central portion of the pad, which induced a tight seal as the soft mutable collagenous tissues at the edge of the pad could conform to any surface.

A skirt of pleated perforate extraxial skeletal material surrounds the pad. In specimens with a wide pad, the pleats are loose, with low amplitudes and long wavelengths in cross section. In specimens with smaller aboral pads, the pleats are much tighter, with deep grooves, high amplitudes and very short wavelengths. This suggests that muscular or mutable collagenous tissues were responsible for wrinkling the surrounding perforate extraxial region. This caused a decrease in the diameter of the aboral pad, puckering it. Extreme examples include a puckered specimen with a 0.6 mm wide aboral pad and flanking pleats that are 1.4 mm wide; a non-puckered specimen shows an aboral pad 2.5 mm wide and pleats that are 0.6 mm wide (Figure 2.16).

Similar aboral attachment pads are encountered in the edrioasteroids *Stromatocystites reduncus* from the Middle Cambrian of Australia (Smith and Jell, 1990), *Totiglobus nimius* from the Middle Cambrian of Nevada (Bell and Sprinkle, 1978), and *Totiglobus? lloydi* from the Middle Cambrian of Utah (Sprinkle, 1985), as well as the helicoplacoids and *Gogia* discussed herein. The edrioasteroid groups have a more tightly sutured skeleton than *Camptostroma,* which would have provided leverage for the aboral pad, as well as a distinct zone delineating the oral and aboral surfaces. The rim was inferred to remain in contact with the substrate while the aboral pad was raised, inducing a seal (Smith and Jell, 1990). *Camptostroma*, like *Totiglobus*, does not have a peripheral

rim, which, along with other characters, has served to exclude it in some systematic studies from the edrioasteroids (Paul and Smith, 1985; Sumrall, 1997; Mooi, 2001).

Because *Camptostroma* lacks a peripheral rim, the pad was flexible in life and capable of "puckering," a phenomenon especially conspicuous in the type specimen (Figure 2.3). The center of the aboral attachment pad is more depressed than the edges, which demonstrates induction of a tight seal without the benefit of a peripheral rim. The type specimen also shows a deep furrow along the edge of the aboral attachment pad, where it abuts the pleated skirt. As Ruedemann (1933) recognized, the animal was likely very flexible, and the furrow is probably a result of compaction of the three-dimensional animal, as the furrow stands out in opposite relief upon the counterpart. Furthermore, the furrow is not seen in any other specimens, including those that appear to be contracted.

A short zone of imbricate plates that connect the pleated skirt to the aboral pad marks the boundary between the two aboral surfaces. These imbricate plates are tangential to the edge of the pad, and extend in a zone approximately 2 mm wide, where they grade into the skirt. The pleats are made of multi-sized plates that, while small, are 2-3 times larger than the small multi-sized plates of the aboral pad, and larger than the imbricate plates connecting the pleats to the aboral pad. Toward the oral surface, these plates increase in size, and grade into small epispire-bearing plates that are not arranged into folds. There is no clear delineation between the aboral and oral surfaces; the clearest demarcation of the boundary between the regions is the border at which pleats meet epispire-bearing plates.

Growth

The Extraxial-Axial Theory (Mooi et al., 1994; Mooi and David, 1997; 1998) also provides a means for studying the growth of echinoderms in each skeletal region. Growth of the axial region is mediated by the "Ocular Plate Rule" (Mooi and David, 1997) wherein ocular or terminal plates sequentially bud off ambulacral elements in an alternating zigzag fashion. The perforate and imperforate extraxial regions were thought to add new plate elements at any place upon the theca, growing without any mediating center or zone. Sprinkle and Guensburg (2001) revised these perceptions of growth in stalked echinoderms in light of the Extraxial-Axial theory. Specifically, they recognized that the boundary between the perforate and imperforate extraxial regions is a growth zone for the imperforate extraxial region, and that the perforate extraxial region grows by budding of new plates along the edges of primaries, to form secondaries, then along the edges of the secondaries to form tertiary plates. These principles guide the following discussion of *Camptostroma* growth.

The axial region follows the same basic premises outlined in Mooi and David (1997); namely that ambulacra grow by alternating terminal plate insertion, and subsequent growth of inserted plates. *Camptostroma* ambulacral cover plates and floor plates are larger near the mouth and smaller toward the tips, indicating distal plates are younger, and floor plates are biserially arranged, which preserves the alternating budding pattern. The ambulacral tips are located near the edge of the oral surface, where they grew away from the mouth by addition of new plate elements. The ambulacra are not free as suggested by Durham (1966, 1968a).

Growth of the superior and inferior interambulacral areas (perforate extraxial region) and ambulacra (axial region) are necessarily coordinated. As ambulacra extended by plate addition, so must have new plates been added at the zone of plate addition at the edge of the oral surface in order to accommodate the lengthening of the ambulacrum. Floor plates are sutured to the adjacent interambulacral plates, locking them in a position that required sequential development via plate growth once inserted. If the ambulacra grew radially at a different rate than that of the bordering interambulacra, it would cause shear between the skeletal regions, damaging the soft tissues that held these regions together. This suggests that the boundary between the perforate and imperforate extraxial regions acted not only as a zone of plate addition for the imperforate axial region (Guensburg and Sprinkle, 2001), but also the axial region at the five points at which the ambulacra abut this zone. This hypothesis is difficult to test because of the rarity of well-preserved oral surfaces upon juvenile specimens. However, only by adding small plates in concert with the ambulacral areas could post-insertion plate growth be accomplished.

As the interambulacra grew, the test became more domal, as suggested by a flattened juvenile specimen with little evidence of the folding so common in flattened adults. The doming was in response to size increase of already inserted plates, which caused the interambulacra to widen despite being bordered by ambulacra that are at a fixed angle. Instead of widening the angle between the ambulacra, growth forced the interambulacral areas to bow outward, which domed the entire oral surface as all interambulacra grew in concert (Figure 2.17).

Because ambulacral plates are smaller distally (relative to the mouth), distal interambulacral plates adjacent and connected to the ambulacra must also be smaller

because of the association with the ambulacral plates. Therefore, despite the fact that the distal edges of each interambulacrum are wider than proximal areas, larger plates (approximately 3 mm in diameter) are found in the narrower areas nearer the mouth, and smaller plates (< 1 mm in diameter) are found peripherally. This is intuitive relative to growth, that older plates are larger than younger plates, but this requires an ever-increasing rate of peripheral plate insertion as the animal grows. Distally, smaller plates make up a greater amount of surface area, requiring an exponential increase in the number of plates added distally to the edge of the oral surface (Figure 2.18). Therefore smaller and smaller plates are required to account for an ever-increasing amount of surface area. As the inferior layer of interambulacral plates lies in direct contact with the superior layer, the inferior plates necessarily grew in the same manner, and show size variability in some specimens.

As *Camptostroma* grew, the ambulacral areas changed from straight to distally curved. Ambulacra A, B, D, and E (designations are according to Carpenter's System, Carpenter, 1884) are straight near the mouth, and curved counter-clockwise distally, whereas the C ambulacrum is straight near the mouth, and curved clockwise distally. Distal curvature of the ambulacra requires the terminal plates responsible for the addition of ambulacral plate elements to insert smaller plates on the inner side of the ambulacrum and larger plates on the outer side. For the counter-clockwise (sinistral) ambulacral areas A, B, D, and E, this would require slower growth of flooring, covering, and adjacent interambulacral plates on the left side of the amb, and faster growth of these elements on the right side of the ambulacrum. For the clockwise C (dextral) ambulacrum, this would require the opposite.

Timing of the growth of the ambulacral tips was responsible for ambulacral curvature. After individuals reached a particular size, age, or growth stage, the oculars began asymmetric growth, causing the ambulacra to curve. Adjacent interambulacral plates must have grown differential growth as well, again to avoid shear between the ambulacra and adjacent interambulacral areas. Therefore, interambulacral plates within the curve are smaller, and the interambulacral plates outside of the curve will be larger. Each interambulacrum then will have large plates abutting the outer curve of each ambulacrum, and small plates abutting the inner curve of the other, with plating grading from one type to the other. However, the anomalously curving ambulacrum C (counterclockwise) poses a spatial problem in terms of growth of the CD interray. The interray is bounded by the inner curves of two ambulacra, and the BC interray is bounded by the outer curves of two ambulacra. Furthermore, the tips of the C and D ambulacra in mature specimens are oriented toward one another, generating ambulacral and adjacent interambulacral elements. As they inserted new plates over time, the CD interray grew disproportionately larger, and the BC interray grew disproportionately smaller (Figure 2.9, for example). The extra space accorded by this curvature is probably related to the presence of the hydropore and anal pyramid in the CD interray, but it is not possible to discern whether the anomalous curvature and therefore accommodation space accorded by the C ambulacrum followed the development of the orifices in the CD interray, or whether the orifices followed the development of the curved ambulacrum.

The derived edrioasteroids *Lebetodiscus*, *Foerstediscus*, and *Streptaster* (Bell, 1976) avoid this problem by evolving ambulacra that all curve counterclockwise distally. The ambulacral tips lie fixed and bud off plates at an angle, a consequence of

asymmetrical growth. As the animals grew from the tips of the uniformly curved ambulacra and surrounding interambulacra, the theca spiraled upward as they grew. As these groups have counterclockwise oriented ambulacral tips, the resulting organism is wound into a left-handed spiral. Bather (1900) figured and discussed *Gomphocystis tenax*, a diploporan that converged on this bauplan, but did so with clockwise (dextral) curved ambulacra along the edge of the oral area. This orientation subsequently wound the body into a right-handed spiral. The specimen figured lacks the brachioles commonly found in diploporans, leading Bather to surmise that the spiraling growth presented an alternative to brachioles as an adaptive extension of surface area dedicated to feeding.

The aboral surface grows in two distinct zones, one corresponding to the aboral attachment pad, and the other corresponding to the pleated skirt. Contrary to the growth pattern discussed in Guensburg and Sprinkle (2001), new plates comprising the pleated skirt are inserted at the boundary between the aboral pad and the junction with the pleated skirt, as shown by an increase (from less than 0.25 mm plate diameter to approximately 1 mm plate diameter) in ossicle size away from the zone (Figure 2.19). The largest plates arranged in pleats abut small epispire-bearing oral surface plates. The second zone of aboral growth is located at the center of the aboral pad. The interior of the pad in some specimens shows smaller imbricate plates located at the center (Figure 2.16); these grade to larger imbricate plates fringed by smaller plate elements at the edge of the pad. This suggests growth may have occurred at the center of the pad, and plates radiated outward as "juvenile" plates displaced them. The lower edge of the pleated skirt also increased in size over the life of the organism, as widening of the diameter of the aboral pad necessitated widening of the pleated skirt. Considering its flexibility, it is not possible to

discern a standard pleat size, but the number of pleats is nearly consistent (approximately fifty) in specimens of all sizes, suggesting a set number of pleats that become enlarged over the life span of the animal.

Guensburg and Sprinkle (2001) discerned two zones of plate insertion in addition to the growth at the ambulacral tips discussed by Mooi and David (1997, 1998); the boundary between the perforate extraxial and imperforate extraxial regions, which acted as a zone of plate addition for the imperforate extraxial region, and the spaces between large primary perforate extraxial plate elements. The growth of the attachment surface was not discussed, probably because of the small size in the attachment structures in the eocrinoid and crinoid specimens studied. Similar large aboral suction pads in other taxa also likely grew from the center toward the edges. The pads of *Camptostroma* then are broadly homologous to the suction pads of *Helicoplacus*, *Gogia*, and the lepidocystids. The cylindrical holdfasts of stalked echinoderms and the tapered lower pole of *Helicoplacus,* and the aboral skirt if *Camptostroma* are then likely homologous structures. This calls into question the assertion made by Guensburg and Sprinkle that the boundary between the perforate extraxial and imperforate extraxial regions is a plate generative zone for the imperforate extraxial region. This is true for two of the figured specimens, the Late Ordovician crinoid *Tryssocrinus endotomitus,* and the coeval eocrinoid *Eumorphocystis multiporata*, but not necessarily for the third figured specimen, the Middle Cambrian eocrinoid *Gogia palmeri*. Examination of figures of the type specimens of *Gogia palmeri* in Sprinkle, 1973, as well as specimens of *Gogia* included herein show a holdfast with smaller plates toward the tip (independent of the small plates making up the attachment pad), and larger plates toward the junction with the theca.

Therefore the holdfasts in the *Gogia* eocrinoids inserted new holdfast plates at the junction of the aboral pad and the holdfast, strengthening the arguments for homology of the holdfasts of *Gogia*, the lower pole of *Helicoplacus*, and pleated skirt of *Camptostroma*, as well as for homology of the aboral suction pads in all three taxa.

Therefore, *Camptostroma* had four distinct growth zones, rather than the three suggestive of the work of Guensburg and Sprinkle (2001); the axial and perforate extraxial generative zone at the juncture of the tip of the ambulacrum and the interambulacra, a second perforate extraxial generative zone at the juncture of the oral and aboral surfaces, an imperforate extraxial generative zone responsible for the pleated skirt at the junction of the skirt and aboral pad, and a second imperforate extraxial generative zone located at the center of the aboral pad (Figure 2.20).

Paleoecology

The depositional environment indicated by the rocks that *Camptostroma* is found in is interpreted as off shelf, receiving siliciclastic material from debris flows derived from the shelf above (Stose and Stose, 1944; Taylor and Durika, 1990). The rock varies from mudstones to friable siltstones to fine-grained phyllites. The metamorphosed rocks are more common in the York area, and despite the assertions of Stose and Stose (1944), the metamorphic processes have not entirely destroyed the *Camptostroma* fossils preserved in this unit. Almost universally, however, the fossils are distorted, as are trilobites (Campbell and Kauffman, 1969).

Camptostroma has a flexible aboral attachment pad, which induced a tight seal with hard or semi-lithified substrates. The inferred hard substrate is skeletal debris, most

often from molting arthropods, particularly trilobites. Many other Cambrian echinoderms are found attached to the isolated cephalons of trilobites (Sprinkle, 1973; Wilbur, 2004, and herein), and considering the abundance of trilobites in the Kinzers Formation (Resser and Howell, 1938; Campbell and Kauffman, 1969), this is the most likely attachment surface. The size of *Camptostroma* likely would restrict the animal from adhering to any but the largest trilobite cephalon. The aboral attachment pad varies from 0.6 cm to 4.0 cm wide, depending on the state of contraction of the specimen upon which it is found. Trilobites in the Kinzers Formation have cephalons that grow to sizes of up to 3.2 cm in length and 6.0 cm in width (type specimen of *Wanneria walcottana* [Resser an Howell, 1938]), suggesting that these were indeed suitable substrates for attachment. None have been found attached, but considering the flexibility of the pad and paucity of other suitable hard substrates, it is likely that *Camptostroma* attached impermanently via suction.

It has been suggested that the early echinoderm *Stromatocystites pentangularis* attached to substrates via collagenous cement rather than by suction (Parsley and Prokop, 2004). Were this the case for *Camptostroma* and other Early Cambrian groups, there would be a wealth of trilobite material with cemented echinoderm structures, as is common with Ordovician groups attached to hard grounds. The lack of disembodied Camptostroma skeletal material attached to trilobite debris again suggests the presence of an aboral suction pad, which is also the more likely mode of attachment pad in *Stromatocystites pentangularis*.

Camptostroma has well defined epispires on its oral surface, which supplemented the water-vascular system in performing respiratory functions. The tube feet were used

primarily for feeding on food particles raining down from above or delivered via currents. The domal shape of the oral surface extended the ambulacra some distance into the water column, and allowed food collection from any angle, rather than just from above. Tube feet collected food particles and passed them into the food groove, which then carried them using cilia toward the mouth. These animals vary greatly from other Early Cambrian echinoderms in that they are closer to the sediment-water interface, but this was not necessarily restrictive because of the environment of deposition. The grain size of the rock in which *Camptostroma* is found is the largest of any of the Early Cambrian groups, which suggests the possibility of a higher energy depositional environment than found in other Early Cambrian echinoderm paleoenvironments. Higher energy currents are capable of carrying larger loads, including larger food particles than those expected in lower energy environments. This would have allowed *Camptostroma* to flourish despite being so close to the sediment-water interface, and despite lacking brachioles, contrary to the adaptive strategies of other Early Cambrian echinoderms.

Bottjer et al. (2000) and Dornbos and Bottjer (2000, 2001) discussed the exceptional preservation of helicoplacoid echinoderms of the Early Cambrian of eastern California, which was the result of periodic obrution deposits borne of large tropical storms along the coast of paleoequatorial Laurentia. This rapidly buried the organisms, which thrived in sediments with a sparse infaunal population. The lack of burrowers created a sharp sediment-water interface, which as a consequence was anoxic immediately below the surface. Thus, any specimens buried were unlikely to be disturbed by burrowers or scavengers, which could not survive in this environment. X-radiograph studies of the rocks in which helicoplacoids are found show evidence of

microbial matgrounds overlain by graded beds, which supports this premise. No similar sedimentological studies have been carried out for the Lower Member of the Kinzers Formation, but it is probable that *Camptostroma* was preserved in a similar manner. First, the theca of *Camptostroma* is flexible and composed of myriad plates, and second; many specimens are partially disarticulated, which shows that soft tissues held the plates together.

Brett et al. (1997) conducted a study of taphonomic types of echinoderms, wherein the authors created three bins for the spectrum of skeletal element suturing in echinoderms. *Camptostroma* corresponds to "Group One" which is characterized by lightly sutured plates. Also included in this group are ophiuroids, "carpoid" echinoderms, asteroids, paleoechinoids, eocrinoids, (Brett et al., 1997), and helicoplacoids (Dornbos et al., 2001). These echinoderms are only rarely preserved as body fossils, and are more likely to be preserved as single plate elements. Specifically, asteroid echinoderms begin to experience loss of soft tissues six days after death, and experience total loss by 17 days after death (Schafer, 1972; Donovan, 1991; see section on helicoplacoids herein for further discussion of preservational types), suggesting the unlikelihood that body fossils are preserved in anything but mass-mortality events wherein organisms were quickly buried. Furthermore, a fairly diverse soft-bodied fauna exists in the lower member of the Kinzers Formation, including *Tuzoia*, *Anomalocaris pennsylvanica*, and *Serracaris* (Resser and Howell, 1938; Hagadorn, 2001; Liberman, 2003). Because of the fragile nature of the flexible test of *Camptostroma*, and the additional soft-bodied faunal components, the Kinzers represents one of the Cambrian Lagerstätten, for which obrution deposits are the most likely culprit in their preservation. Because of the off-shelf position

of the depositional environment of the Kinzers Formation, it is more likely that these fossils were buried by periodic submarine sediment flows in a fashion similar to that inferred to be responsible for the exceptionally preserved Middle Cambrian Burgess Shale (Fletcher and Collins, 1998) of eastern British Columbia, Canada. *Camptostroma* preservation is then akin to the exceptional preservation of helicoplacoids discussed by Dornbos and Bottjer (2000, 2001).

Systematic Position

Upon the redescription of *Camptostroma* as an echinoderm by Durham (1966), the animal was placed in the monotypic class Camptostromatoidea Durham, 1966. This designation was made based on the misunderstood anatomy as described by Durham (1966, 1968a), in which the fossil was assumed to be a floating medusiform echinoderm with free arms and misdiagnosed oral and aboral areas. Durham considered the group to be closely allied with class Holothuroidea, based on the similarity of *Camptostroma* epispire cover plates to holothurian spicules.

The bi-layered oral surface of *Camptostroma* is unique in Echinodermata. Paul and Smith (1984) discussed secondary interambulacral plating, but the inferior cobblestone pavement of plates is not figured or mentioned. Rather, the authors in discussing secondary interambulacral plates meant the epispire-bearing plates and flanking epispire cover plates. This was used as a character excluding *Camptostroma* from other Edrioasteroidea, highlighting its exclusion from the group. This same diagnosis of plating reoccurs in phylogenetic analyses of Cambrian edrioasteroids and related taxa conducted by Smith and Jell (1990), and of Class Edrioasteroidea carried out

by Guensburg and Sprinkle (1994). Bell (1980) and Derstler (1981, 1985) argued that *Camptostroma* showed other edrioasteroid synapomorphies, and should therefore be included within the edrioasteroids. Bell was the first to do so in a Linnean taxonomic scheme, while Guensburg and Sprinkle (1994) were the first to reassign *Camptostroma* to Class Edrioasteroidea in a phylogenetic study based on the revised morphology. This included the discussion of the basal disc used for attachment via suction similar to that seen in other edrioasteroids (Guensburg and Sprinkle, 1994), which was misinterpreted an inverted cone by previous authors (Paul and Smith, 1984; Smith and Jell, 1990; Peterson et al., 1990). Therefore, Class Camptostromatoidea was considered invalid, while the Order Camptostromatoidea Durham, 1966, and Family Camptostromatidae Durham, 1967, were not affected by the transfer to Class Edrioasteroidea (Guensburg and Sprinkle, 1994).

Class Edrioasteroidea Billings, 1858 was diagnosed by Regnéll (1966) as echinoderms with multiplated surfaces, a pentameral endothecal ambulacral system, no arms or brachioles or stalk, anal opening in the posterior interambulacrum (CD interray) covered by a pyramid of lath-shaped plates forming a valve, a hydropore situated between the mouth and anus, and no thecal pores. This description however excludes those taxa with epispires upon the interambulacral surfaces. These include the additional Cambrian Edrioasteroid taxa *Cambraster* (Termier and Termier, 1969; Jell et al., 1985), and *Stromatocystites* (Pompeckj, 1896; Schuchert, 1919; Termier and Termier, 1969; Paul and Smith, 1984; Smith, 1985; Smith and Jell, 1990). Epispires are lost in edrioasteroids by the Late Cambrian (Smith, 1985), while eocrinoids loose them by the Early Ordovician (Sprinkle, 1973) as a consequence of development of thin plating or

other respiratory structures. Expression of this trait in edrioasteroids and eocrinoids suggests common ancestry of the character. Because many early edrioasteroids in addition to *Camptostroma* have epispires, the latter should not be excluded from the Edrioasteroidea based on this character.

This premise is reflected in a revised diagnosis of the class by Bell (1976). Edrioasteroids are diagnosed as follows: polyplated thecate echinoderms with anal structure in the posterior ambulacrum (CD interray), triradiate or pentameral symmetry ("2-1-2" arrangement) with mouth central, endothecal ambulacral system composed of cover plates and floor plates, hydropore located near right posterior side of the oral area (CD interray), accessory hydrovascular passageways common, and irregular interambulacra. Based on these revised characters, *Camptostroma* is clearly an edrioasteroid, and was only placed in a separate class by Durham (1966) because of misdiagnosis, which persisted and affected more recent taxonomic studies.

The presence of epispire cover plates is not unique in Echinodermata. Those found in *Camptostroma* are small and were held in place by soft expansible tissues, and would therefore be amongst the first skeletal elements to be lost during decay. It is possible that the epispires of *Gogia*, a more tightly sutured early Cambrian echinoderm, were covered in all groups, but because of biases in the record, are only recorded in the unique case of *Gogia (Alanisicystis) andalusiae*. The middle Cambrian eocrinoid *Acanthocystites briareus* Barrande, 1887 also has epispire covers (Ubaghs, 1968b), suggesting that these may be plesiomorphic in epispire-bearing echinoderms, and therefore ancestral to edrioasteroids.

Ambulacral cover plates in *Camptostroma* are virtually identical to those found in helicoplacoids (herein) and *Stromatocystites* (Paul and Smith, 1985; Smith and Jell, 1990), the only difference being the irregularity in shape of *Camptostroma* cover plates. This may result from the paucity of *Camptostroma* specimens and the relative abundance of helicoplacoids; some juvenile helicoplacoid cover plates appear irregular, while it is clear that adults have polygonal plates. Analysis of further *Camptostroma* specimens may show more regular ambulacral cover plates. The overall similarity of the ambulacral cover plates in these groups suggests a close relationship between the three groups, and is again suggestive of this being an plesiomorphic character for Echinodermata.

The most significant diagnostic characters in *Camptostroma* are the presence of a pleated skirt of plates surrounding the aboral pad, and the presence of an inferior as well as superior sheet of interambulacral plates. Because of these unique and disparate characters, there is no need to revise the ordinal level status accorded to the group, but as the class, order, genus, and species were improperly diagnosed first by Resser (1933) and later by Durham (1966), the order, genus, and species require adequate diagnosis herein.

SYSTEMATIC PALEONTOLOGY

PHYLUM ECHINODERMATA de Bruguière, 1791

Phylum Coelenterata, Ruedemann, 1933; Resser and Howell, 1938; Kieslinger, 1939; Harrington and Moore, 1956

Phylum Echinodermata, Durham, 1968a; Derstler, 1981, 1985; Paul and Smith, 1984; Smith and Jell, 1990; Guensburg and Sprinkle, 1994; Sumrall, 1996, 1997; Mooi and David, 1998; Mooi, 2001.

CLASS EDRIOASTEROIDEA Billings, 1858

Class Camptostromatoidea Durham, 1966, 1967

Class Edrioasteroidea, Bell, 1980; Derstler, 1981, 1985; Guensburg and Sprinkle, 1994

ORDER CAMPTOSTROMATOIDA Durham, 1966

Order Stromatocystitida Bell, 1980.

Diagnosis – Edrioasteroids with bi-layered interambulacra, and a pleated skirt of small multi-sized ossicles surrounding a flexible aboral attachment pad. No peripheral rim demarcates the transition from oral to aboral surface.

Discussion –Many other edrioasteroids have an aboral pad that was used for suction adherence, for example *Stromatocystites reduncus* (Smith and Jell, 1990), and *Totiglobus* (Bell and Sprinkle, 1978; Sprinkle, 1985), but both sets of authors did so with a tightly sutured theca and peripheral rim, which provided support in anchoring to hard substrates. *Camptostroma* had a flexible theca, which necessitated a much larger aboral attachment pad. The pad changed shape by constricting or relaxing the surrounding pleated skirt that acted as a sphincter, contracting or expanding the aboral pad.

FAMILY CAMPTOSTROMATIDAE Durham, 1967

GENUS CAMPTOSTROMA Ruedemann, 1933

Type species – Camptostroma roddyi Ruedemann, 1933

Etymology – From the Latin c*ampto*, meaning to bend or bow, and the Greek s*troma*, meaning covering, mattress, or bed. Ruedemann did not discuss etymology, but it can be assumed the name refers to the domal shape of the "bell" described by Ruedemann (1933). The name then means, "Curved covering" rather than "curved beds" as in the connotation of the root *stroma* in the word "stromatolite."

Diagnosis – Camptostromatoid edrioasteroid with small lath shaped to triradiate epispire covers situated in the sutural gaps between adjacent epispire-bearing interambulacral plates. A second inferior layer of interambulacral plates is composed of a cobblestone-like pavement of hemispherical to ovoid plates surrounded by groove-bearing lateral plates. The large cobbles provided support for the superior epispire-bearing plates, and the lath shaped plates provided support for the superior epispire cover plates.

Discussion – The bi-layered interambulacral areas are unique within Edrioasteroidea. It is likely related to the fact that there are epispire cover plates, another unique character for the class. Respiratory tissues existed as interconnected nodes immediately below the large cobblestone plates; each node had several radial branches that wrapped around the edges of the cobbles, through the grooves upon the lath shaped lateral plates, and passed through the epispires of the superior layer of interambulacral plates. These tissues functioned similarly to the tube feet, which were capable of expansion through muscular contraction of the ampullae situated at the base of each tube

foot; the node underlying the cobblestone plate if contracted would expand the radiating branches, forcing them to extrude through the epispires, lifting the epispire cover plates. It is possible then that the water vascular system of the axial region and respiratory tissues of the perforate extraxial region are linked developmentally, a possibility explored in more detail in the section concerning *Polyplacus* in the previous chapter on helicoplacoids.

CAMPTOSTROMA RODDYI Ruedemann, 1933

Camptostroma roddyi Ruedemann, 1933, p. 5, figures 1-2, plates 1-4; Resser and Howell, 1938, p. 212, plate 1, figure 15; Kieslinger, 1939, p. A 89, figure 18; Harrington and Moore, 1956, p. F42-F43, figure 5; Durham, 1966, p U1216-U1220, figures 1-2; Durham, 1968b, p. S627-S631, figures 396-397; Derstler, 1981, p. 72, figure 1; Paul and Smith, 1984, p. 450-452, figure 5.

Type material – Holotype, USNM 85181

Diagnosis – Edrioasteroid with a highly flexible domal oral surface. The widest point of the animal marks the boundary between the aboral and oral surfaces. Ambulacra A, B, D, and E curve counter-clockwise distally, ambulacrum C curves clockwise distally.

Description – The mouth of the animal is central atop the domal oral surface, with five raised ambulacra radiating away toward the edge of the oral surface in a 2-1-2 arrangement. The anal pyramid is located in the CD interray near the edge of the oral

surface, and the hydropore is located in the CD interray adjacent to the mouth, closer to the C ambulacrum. Radiating lath-shaped plates fringe both the hydropore and anus; plates of the anal pyramid stand out in slightly higher relief, forming an elevated periproct.

Ambulacra are composed of biserial floor plates that are narrow in the direction of the axis of the ambulacrum, and wide perpendicular to it. Three series of cover plates cover each ambulacrum; each floor plate has a single primary cover plate, two secondary cover plates, and several tertiary plates. Cover and floor plates are larger near the mouth, and decrease in size distally.

The test is very large; the type specimen is 70 mm wide, and partial specimens equally as wide composed exclusively of interambulacral area suggest they may have been much larger. The skirt area surrounding the aboral pad has 49 pleats in the single specimen in which all pleats are visible; partial specimens suggest that this number is relatively standard in the group. Short stretches of imbricate plates connect the pleats to the aboral pad.

Discussion – Camptostroma shows many characters regarded by echinoderm workers as ancestral to the group (Paul and Smith, 1984; Guensburg and Sprinkle, 1994; Sumrall, 1996, 1997; Mooi, 2001), which consistently results in the placement of the animal at the base of the echinoderm tree along with the helicoplacoids. The cover plates and floor plates in both groups are nearly identical.

The anal and hydropore openings are very similarly constructed. Both are composed of lath-shaped plates, which served as a valve for either opening, and possibly

in the case of the anus, to elevate the structure some distance from the epispires to avoid fouling them with waste.

Etymology – Named in honor of the collector, Dr. H. Justin Roddy of Millersville and Lancaster, Pennsylvania (Ruedemann, 1933).

Occurrence – The type specimen is from a locality in Fruitville, Pennsylvania, 4.8 km (3 miles) north of Lancaster, at the junction of Delp Road and Fruitville Pike. Additional localities are found at road cuts along Pennsylvania State Highway 74, 2.9 km (1.8 miles) northwest of York (in the Shiloh area). The rock that contains the fossils is the lower member of the Lower Cambrian Kinzers Formation, *Bonnia-Olenellus* zone.

Conclusions

1. *Camptostroma* is an early edrioasteroid, which is in accord with the conclusions of Bell (1980), Derstler (1981, 1985) and Guensburg and Sprinkle (1994).

2. The test of *Camptostroma* is divided into distinct oral and aboral surfaces that are equal in lateral extent. The oral surface was domed in life, and supported five curved ambulacra that were set into and constituted part of the body wall. Ambulacra A, B, D, and E curved counter-clockwise, and ambulacrum C curved clockwise. The interambulacral areas were composed of two distinct layers. The superior of these was composed of large epispire-bearing plates fringed by epispire cover plates, which are unique in the Edrioasteroidea. This layer was supported by an inferior layer of cobblestone-shaped plates equal in size to and supportive of the superior epispire-bearing plates, and surrounded by radiating lath-shaped plates, that are equal to in size and supportive of the superior epispire cover plates. This inferior layer of interambulacral

plates is unique in Echinodermata. The aboral surface is composed of two distinct regions. A large central flexible pad was used for attachment to skeletal debris or lithified substrates. This contradicts a past reconstruction by Paul and Smith (1984) of a tapered lower pole inserted in the substrate that was advanced in the literature by Smith (1985), Smith and Jell (1990), and Peterson et al. (2000). The pad was surrounded by a skirt of small multi-sized plates that were arranged into pleats that acted as a sphincter, manipulating the attachment pad.

3. *Camptostroma* skeletal regions grew from four separate zones of plate addition, as shown by skeletal regions with plates that show varying sizes of otherwise identical plating elements. These are: the termination of the ambulacrum, which regulated addition of biserial ambulacral elements (axial region) and adjacent interambulacral elements (perforate extraxial region); the junction of the oral and aboral surfaces, which regulated the addition of interambulacral elements; the boundary of the aboral pad and aboral pleated skirt, which regulated the addition of small multi-sized skirt elements (imperforate extraxial); and the center of the aboral pad, which regulated the addition of the imbricate plates and small multi-sized plates that composed the aboral pad.

4. *Camptostroma* shows characters ancestral to many early Cambrian groups, suggesting a basal position on the echinoderm tree, and may possibly represent as close to a hypothetical ancestral echinoderm as has been discovered yet.

5. Preservation of *Camptostroma* is the result of periodic submarine sediment flows, following the Burgess Shale model. The Kinzers Formation represents a similar case of exceptional preservation similar to that of the helicoplacoid echinoderms and the fauna of the Middle Cambrian Burgess Shale.

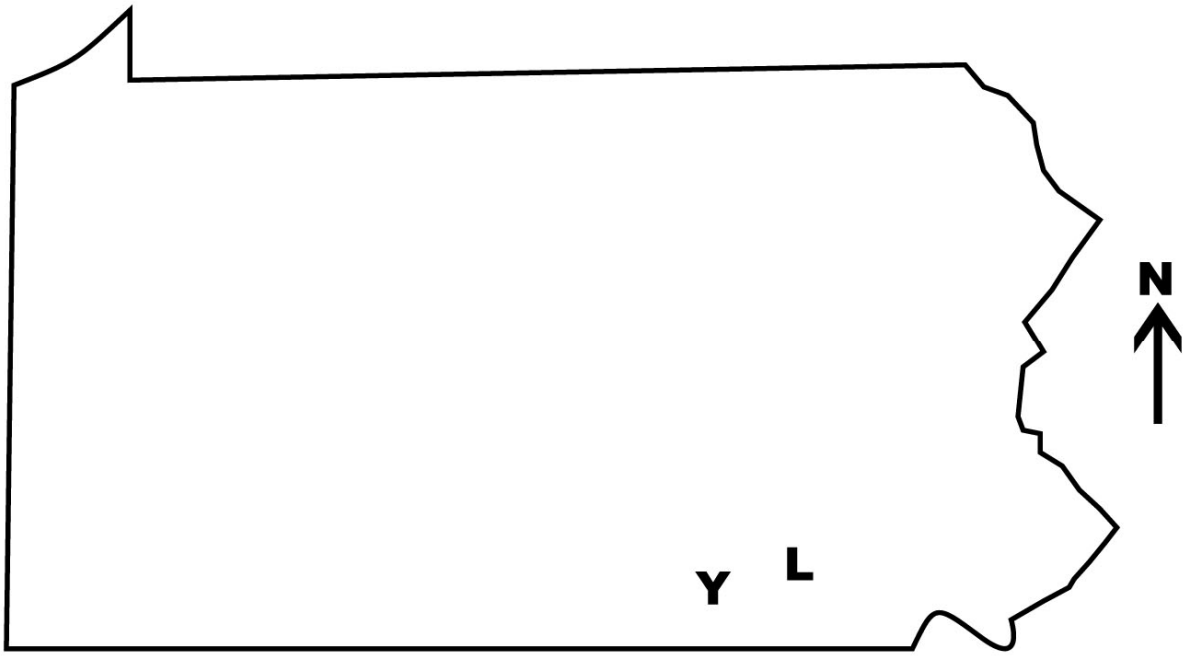


Figure 2.1. The State of Pennsylvania, with York (Y) and Lancaster (L) labeled.

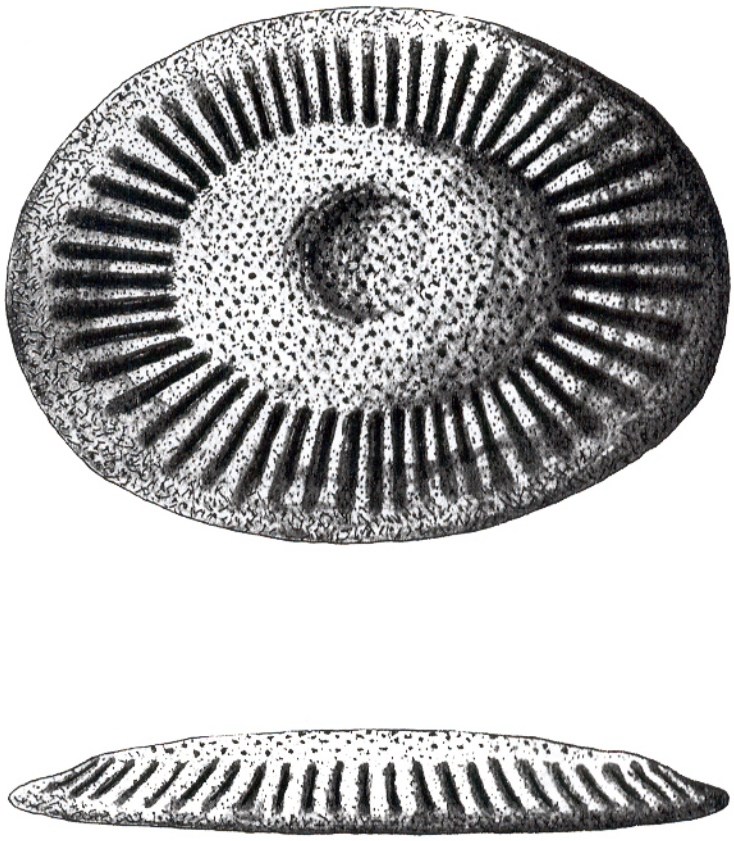


Figure 2.2. *Camptostroma roddyi* Ruedemann, 1933, as figured by the original author (Ruedemann, 1933; Plate 4). The reconstruction follows the interpretation as a schyphozoan. The top is the upper surface; the bottom is a side view. No scale is given, but based on other specimens; the reconstructed animal is approximately 60 mm across in the long dimension.

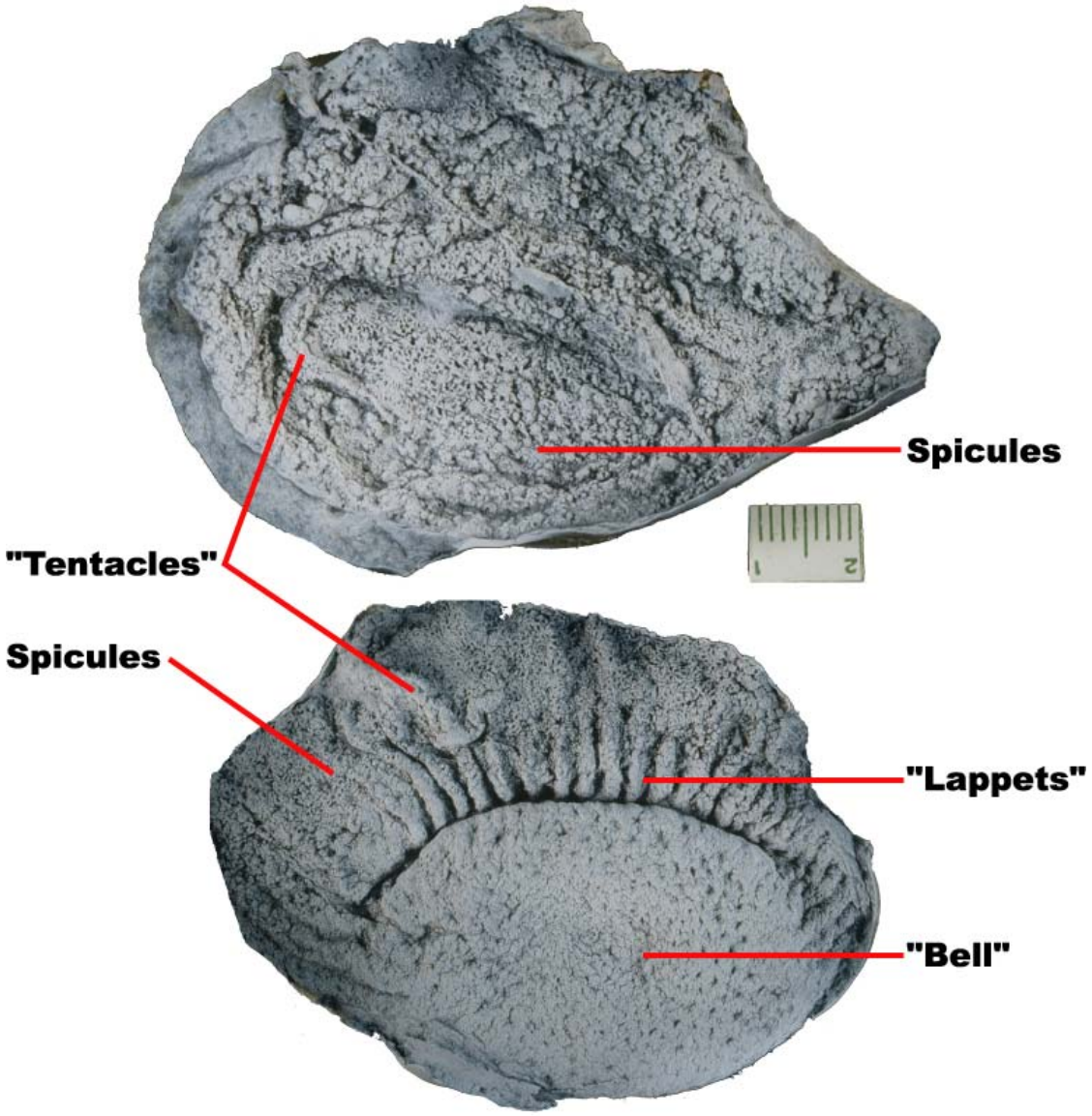


Figure 2.3. USNM 85181, with anatomical features as interpreted by Ruedemann, 1933. Metric ruler for scale.

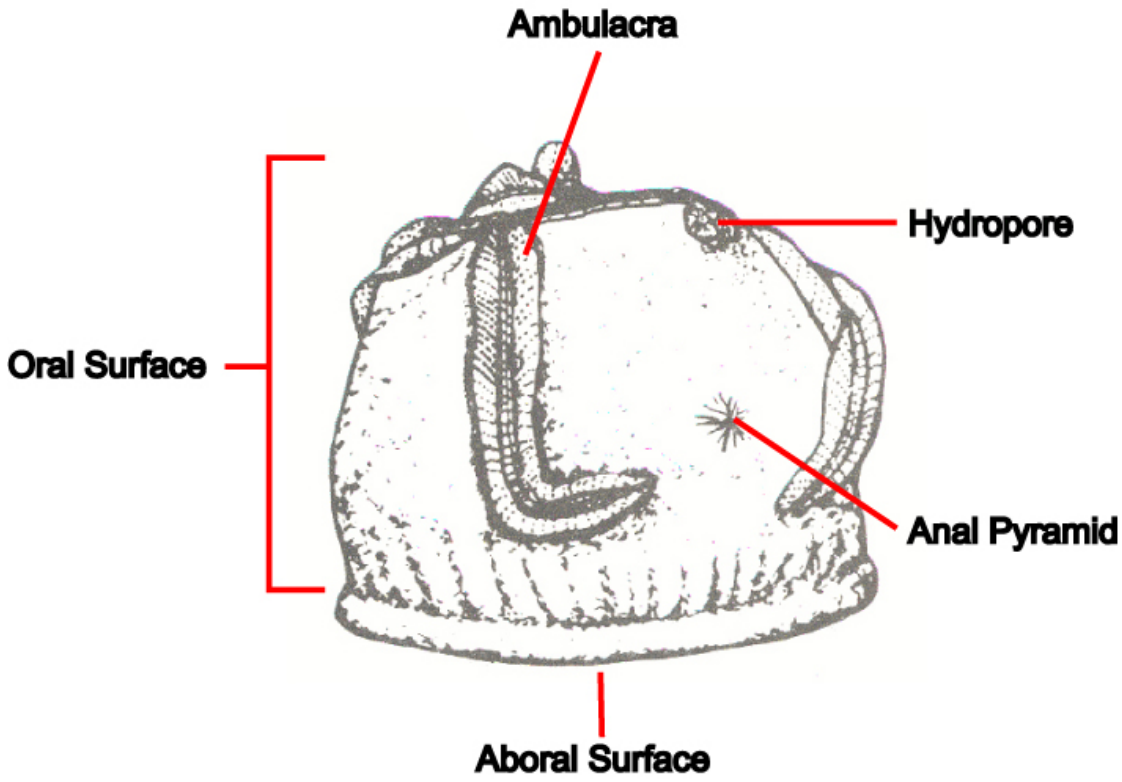


Figure 2.4. *Camptostroma roddyi* Ruedemann, 1933, as reconstructed by Derstler (1981; figure 1). Labels show anatomical features as interpreted by Derstler.

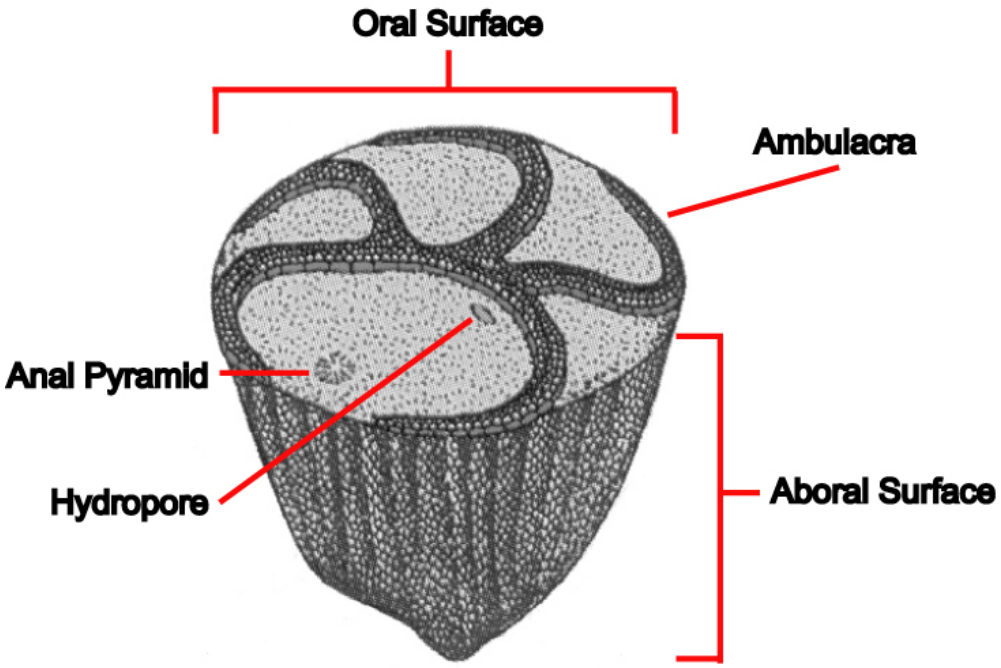


Figure 2.5. *Camptostroma roddyi* Ruedemann, 1933, as reconstructed by Paul and Smith (1984; figure modified from Peterson et al., 2000). Labels show anatomical features as interpreted by Paul and Smith.

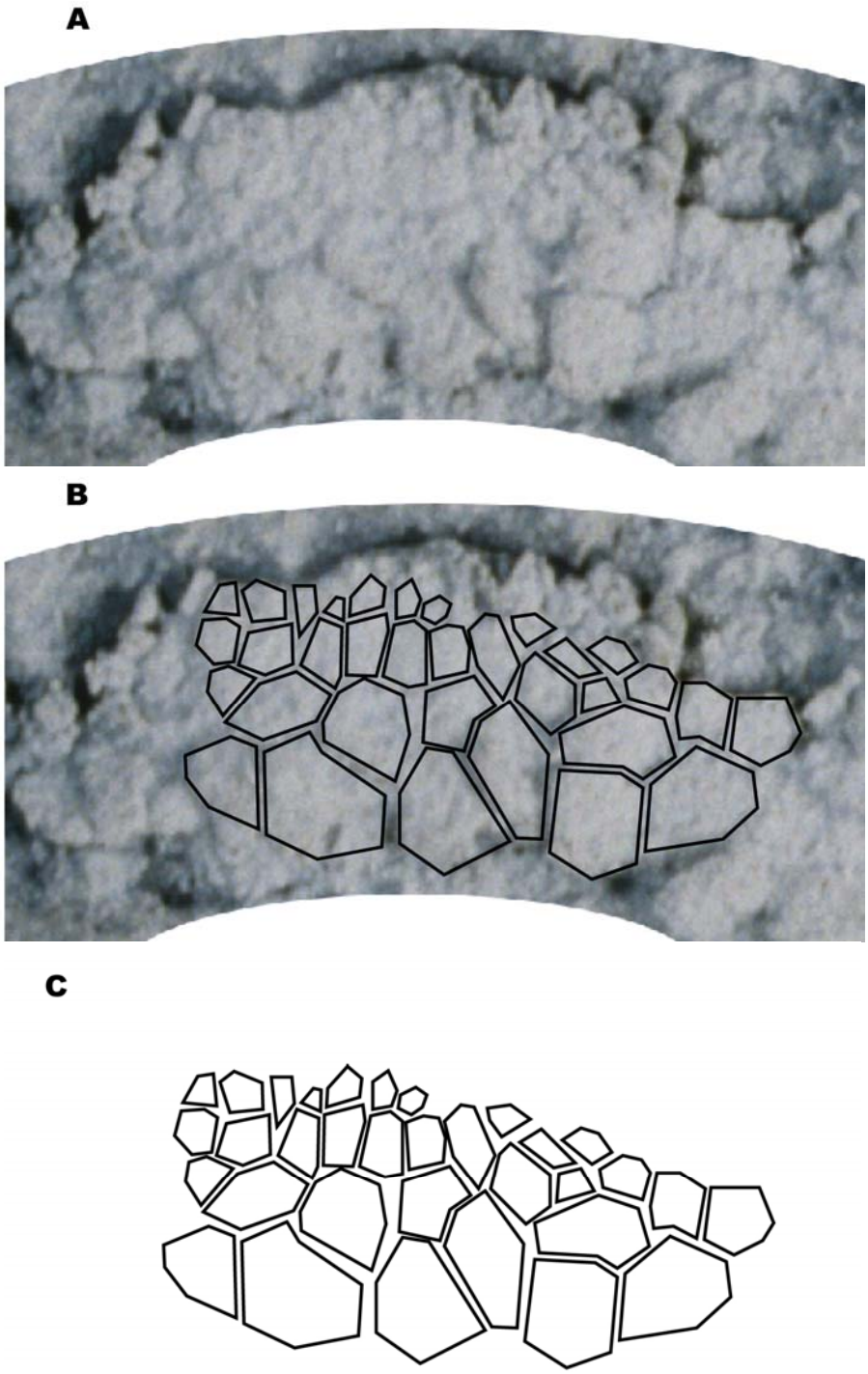


Figure 2.6. *Camptostroma* ambulacral coverplates. A, Photograph of an unnumbered latex cast, Texas Memorial Museum. B, Tracing of ambulacral cover plates. C, Photograph removed. Field of view in A-C is 7 mm wide.

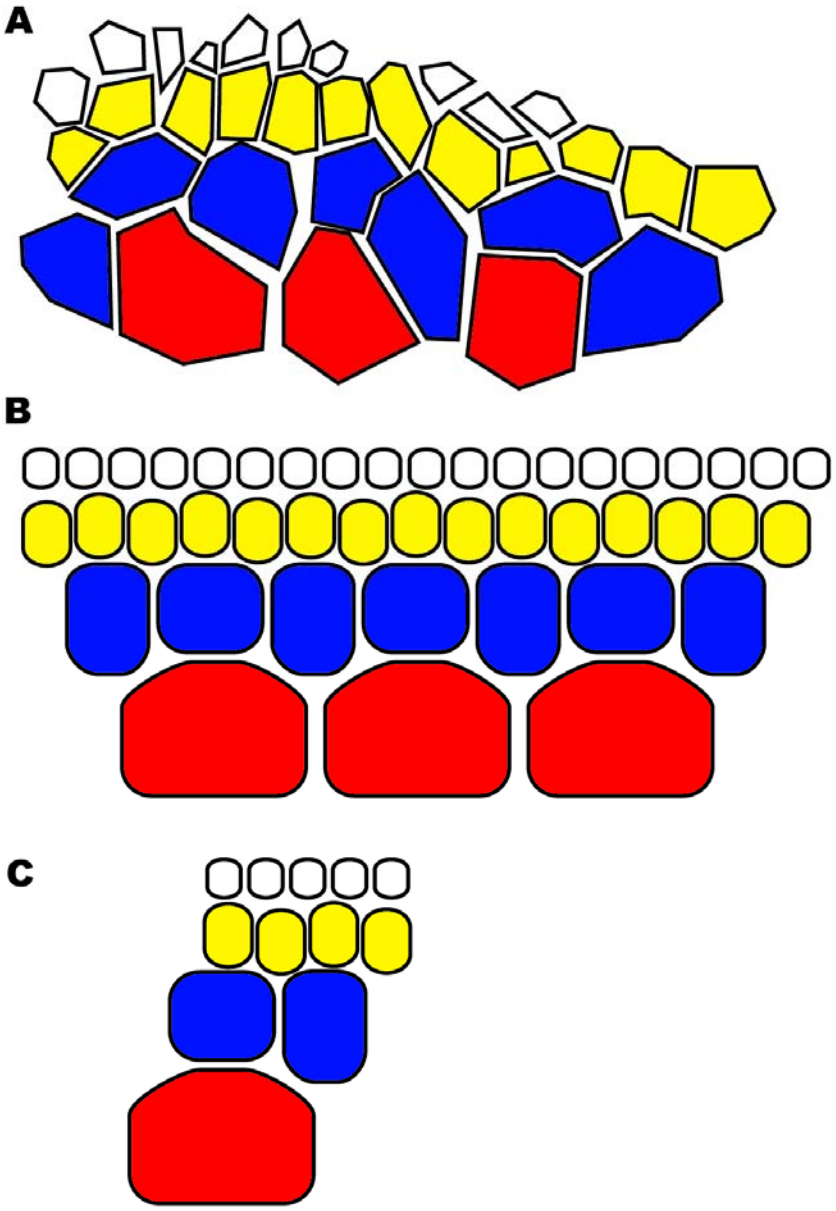


Figure 2.7. Schematic representation of ambulacral coverplates, based on figure 1. A, Tracing of ambulacral coverplates colored to show primary (red), secondary (blue), tertiary (yellow) and quaternary (white) coverplate rows. B, Schematic showing organization of plates. C, Repeating ambulacral unit. Te ratio of plate row to the number of plates in each row is as follows: 1°: 2°: 3°: 4°:: 1:2:4:5. Field of view is 7 mm across.

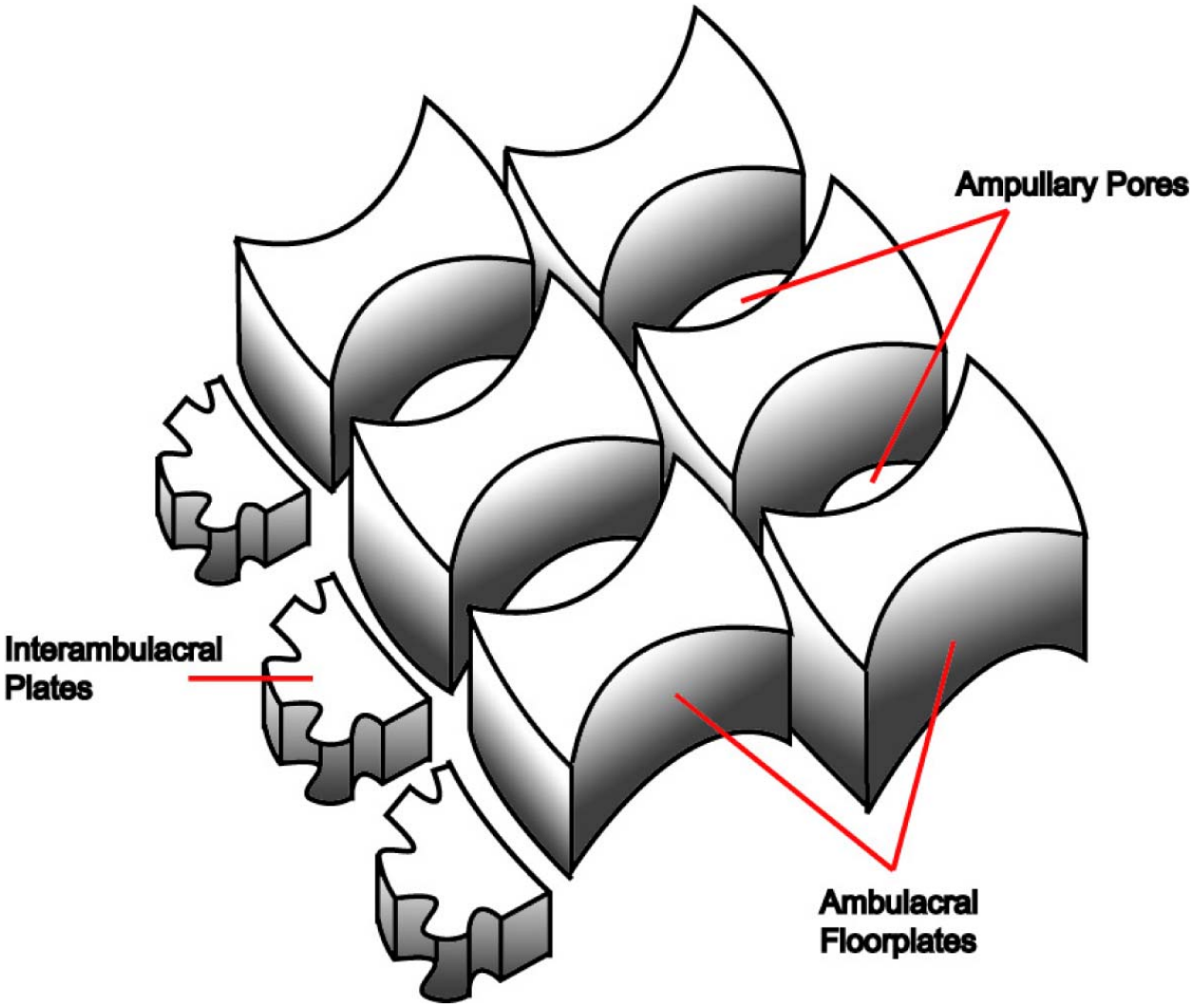


Figure 2.8. Reconstruction of ambulacral floorplates, with coverplates removed. Ambitus is toward the top left of page. Adjacent interambulacral plates are attached near bases of floor plates, allowing ambulacrum to stand out in relief.

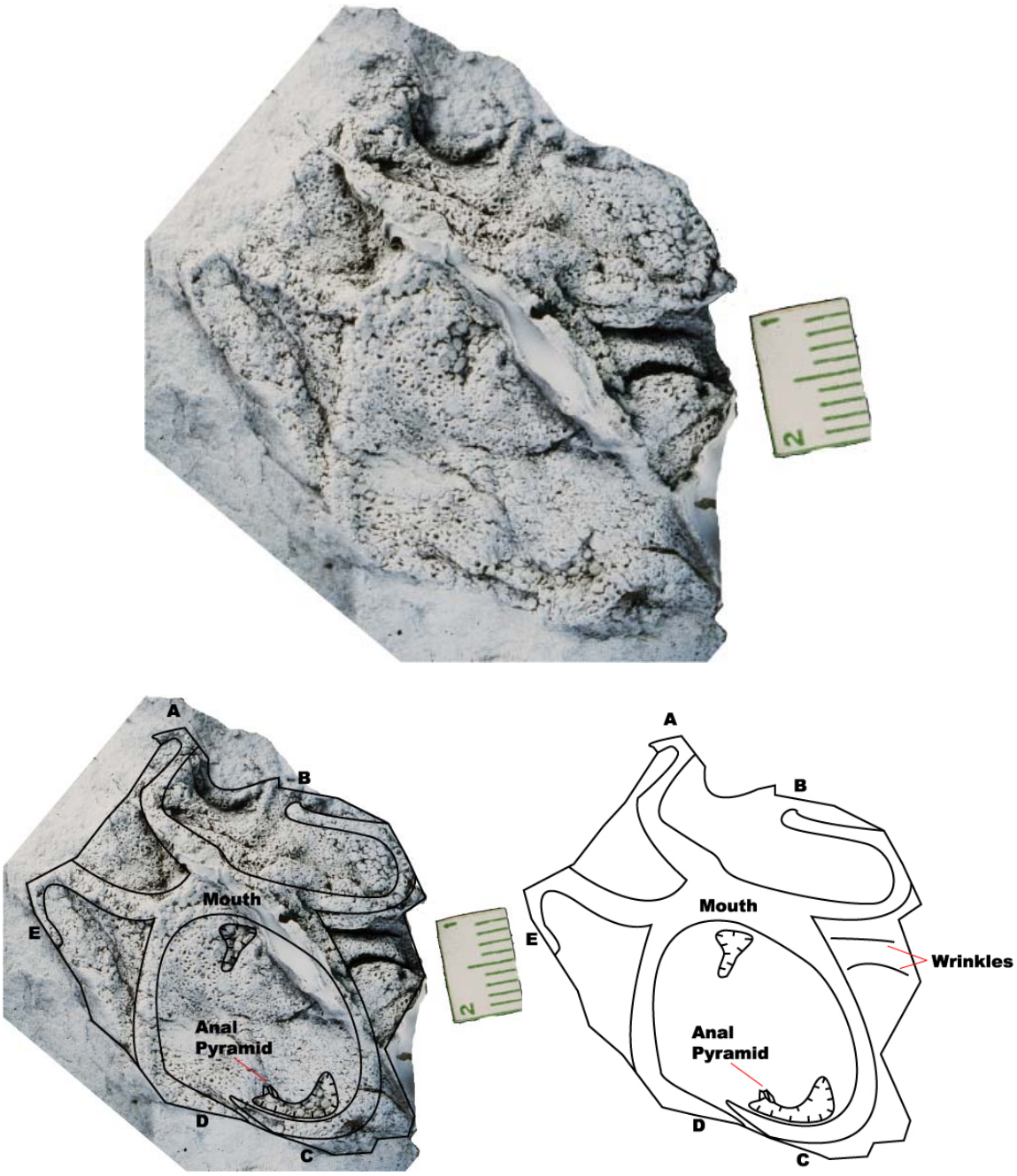


Figure 2.9. Oral surface of unnumbered specimen, USNM. Top specimen is unlabeled; specimen on lower left is a labeled photograph; bottom right is an interpretive tracing of the oral surface, with the photograph removed. Ambulacra are labeled according to Carpenter (1884). Ambulacra A, B, D, and E curve counterclockwise, while C curves clockwise. This specimen also shows the "2-1-2" branching pattern of ambulacra at the mouth, and the anal pyramid near the edge of the aboral pole. Portions of the surface are badly wrinkled by compression of the domed oral surface, particularly the BC interray. Hachured areas within the CD interray show places where taphonomic processes have excavated the superior layer of interambulacral plates, exposing the inferior layer.

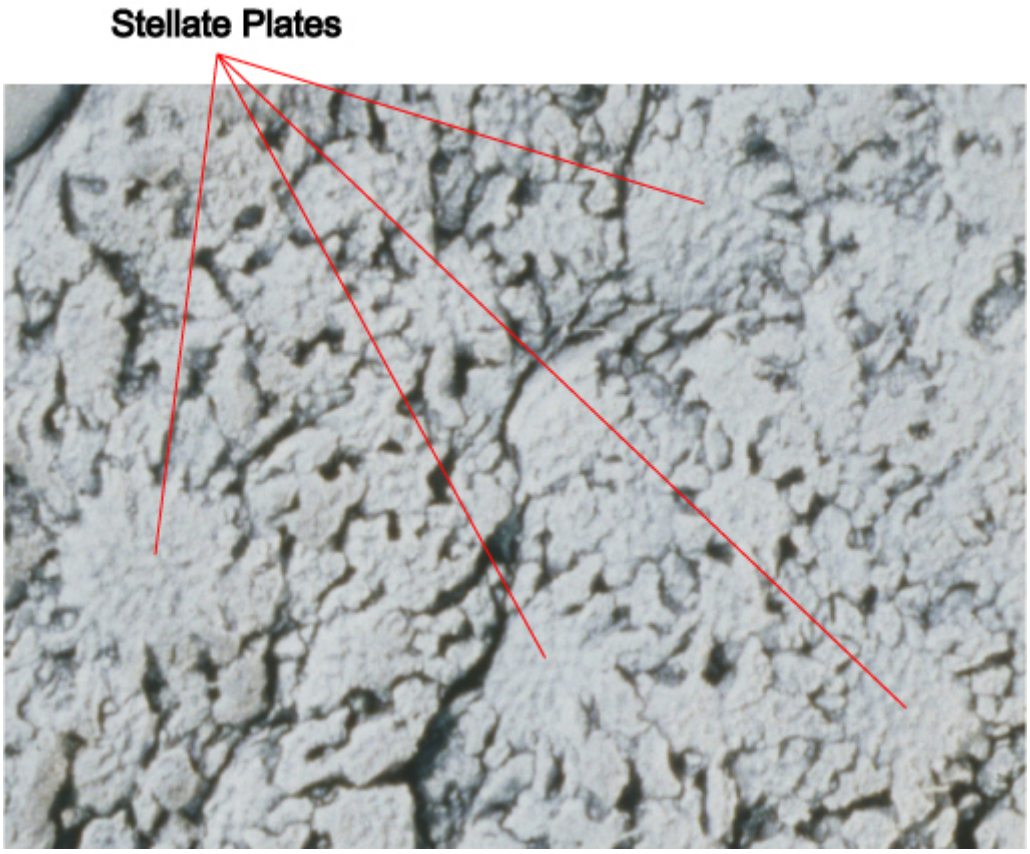


Figure 2.10. Epispire-bearing “stellate plates” from the CD interray of an unnumbered USNM specimen. Field of view is 10 mm wide.

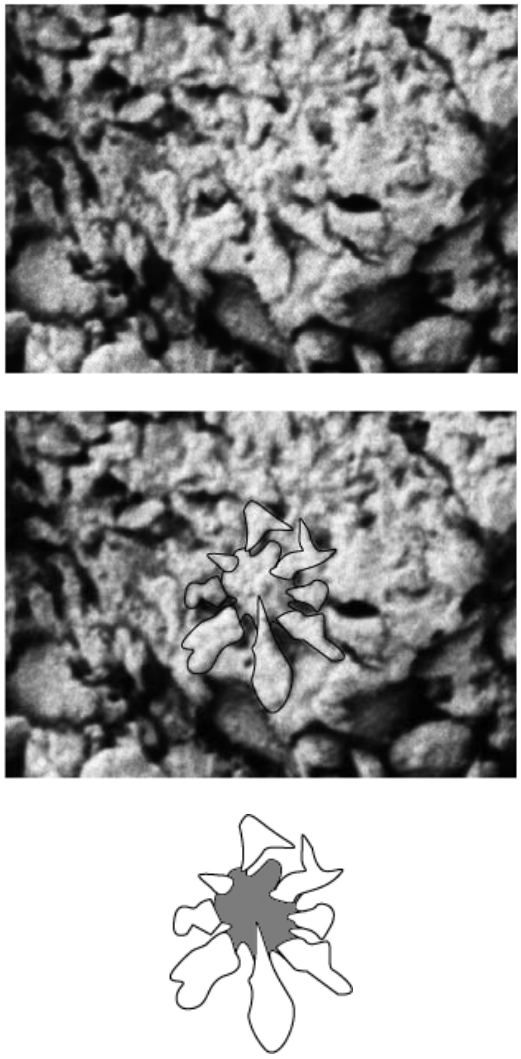


Figure 2.11. Epispire coverplates, from an unnumbered specimen in the USNM collections. The epispire-bearing interambulacral plates (gray in illustration) are fringed by irregularly shaped ossicles that covered the respiratory tissues below. Plate is approximately 2 mm wide.

Figure 2.12. Inferior interambulacral layer, composed of cobblestone plates fringed by lath-shaped plates, some of which bear grooves. Field of view is 16 mm across.

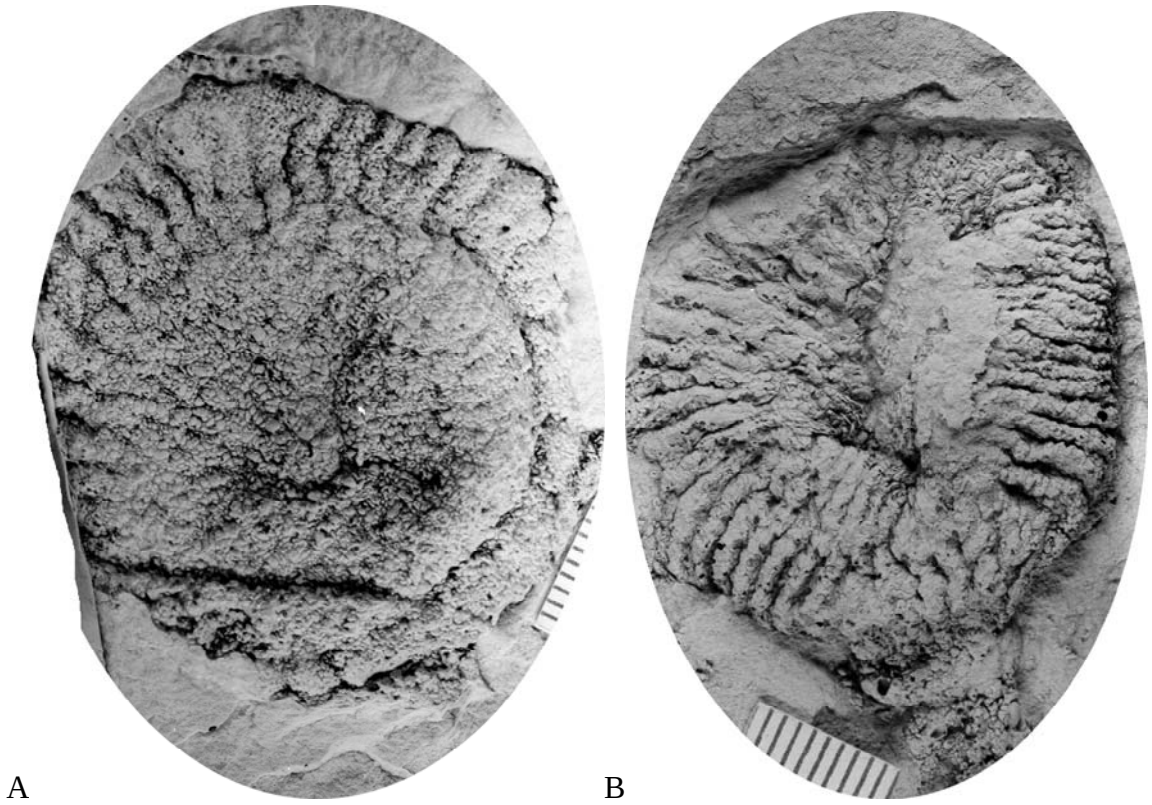
A

B

Figure 2.13. Anal pyramid. A, Anal pyramid in unnumbered specimen in TMM collections; field of view is 8 mm wide. B, Anal pyramid in unnumbered USNM specimen; field of view is 9 mm wide. Both shoe radiating lath-shaped plates, but only B shows relief.

Figure 2.14. *Camptostroma* hydropore, located in CD interray of USNM 85181. Red box shows approximate area magnified to right. The hydropore shows negative relief.

Figure 2.15. Aboral surfaces in external (left) and internal (right) views. When contracted, the smaller plates surrounding the imbricate plates pucker and cover the imbricate plates, the contracted specimen having a dimpled appearance (see aboral surface of holotype, Figure 3). Unnumbered USNM specimen; field of view is approximately 40 mm across.



A B

Figure 2.16. Expanded (A) and contracted (B) aboral areas of two specimens of *Camptostroma*. Specimen A was not actively attached when buried, while B was likely moored to a hard substrate immediately before being uprooted and buried. Note the differences in the diameter of the aboral pad, and the tight folds of the pleated skirt in specimen B. A is PE 366 (North Museum) and B is PE 29A (North Museum). Part of a metric ruler is in each photograph for scale.

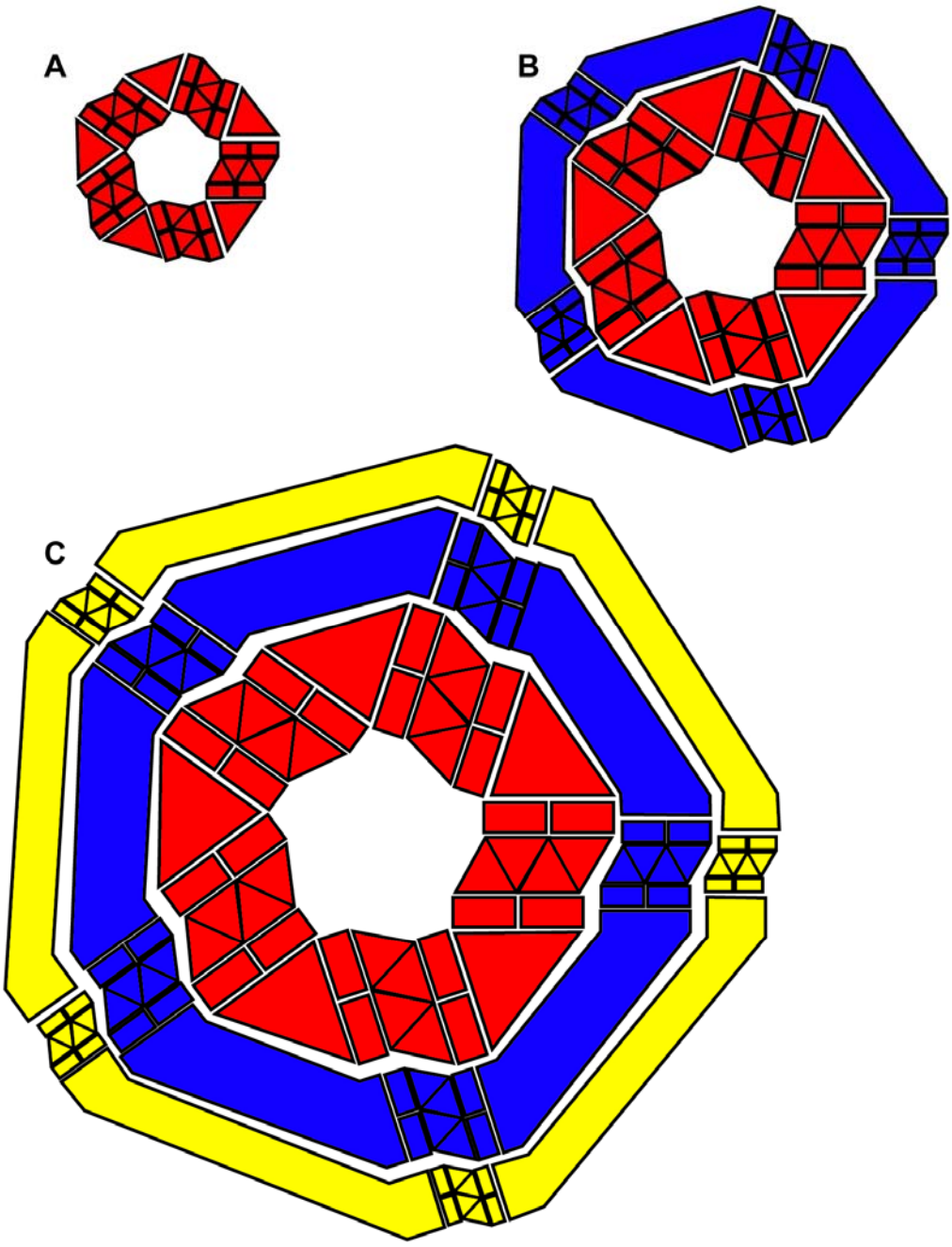


Figure 2.17. Interambulacral growth in *Camptostroma*. Biserial triangles represent ambulacral plates; adjacent rectangles represent adjacent interambulacral plates; polygons in between ambulacra represent interambulacral areas. A-C show three generations of plate growth (1st generation is red, 2nd is blue, 3rd is yellow). Interambulacral areas become larger away from the origin, leaving more surface area to be compensated for by smaller plates, requiring an exponential increase in the rate of plate addition.

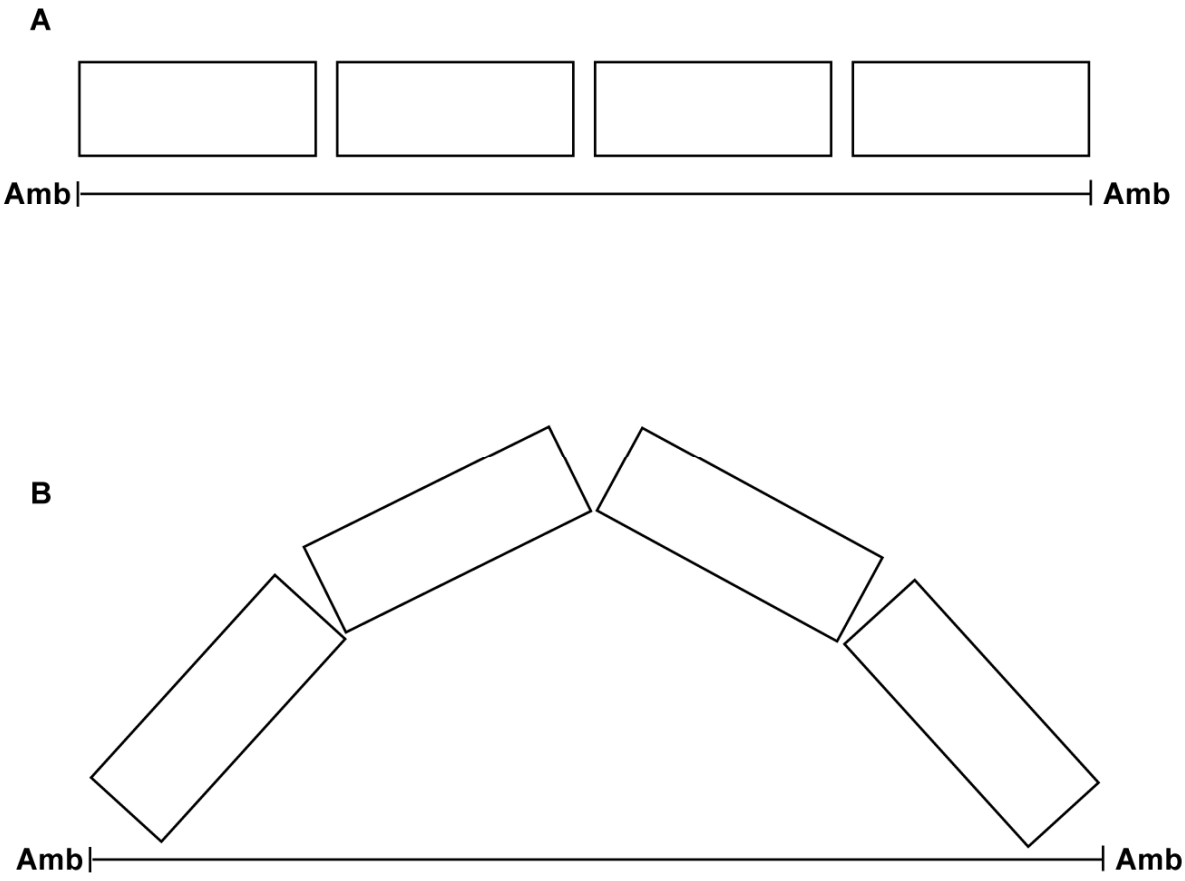


Figure 2.18. *Camptostroma* interambulacral doming in cross section. The distance between the ambulacra is set at 72º by the rules of pentamery. As interambulacral plates grow laterally, the surface responds by bowing outward to accommodate the extra length. This phenomenon explains the proximal cause for the domal shape of the theca. A represents a flattened profile juvenile in cross section; B represents a domal adult.

Figure 2.19. Pleated aboral skirt; pad is to the bottom left. Plates were inserted at the edge of the pad, and grew larger toward the edge of the oral surface, or to the upper right in this picture. Field of view is 7 mm wide; photo is of is an unnumbered North Museum specimen.

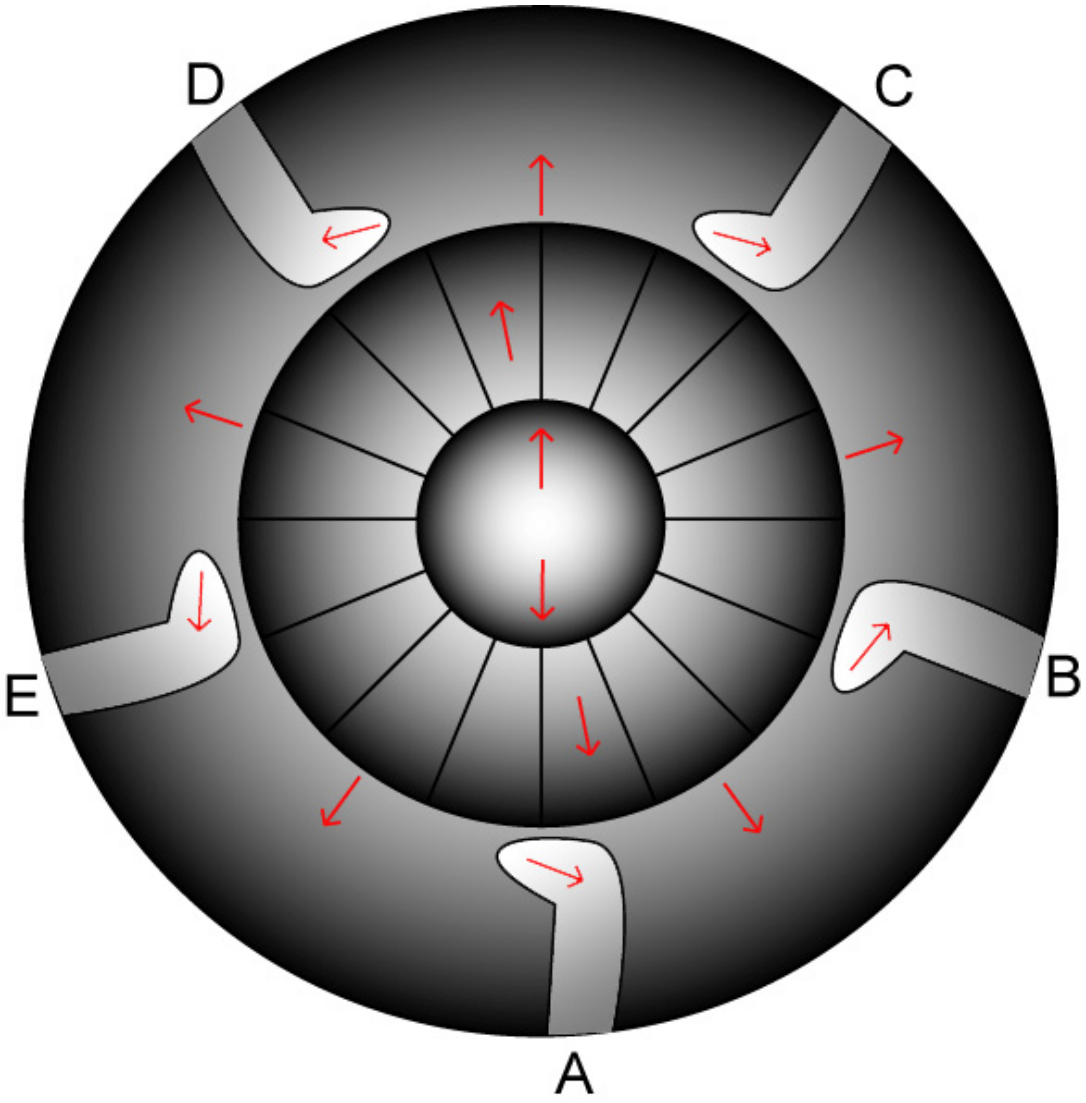


Figure 2.20. Camptostroma growth portrayed in a polar projection, aboral surface central. Four zones are recognized: the aboral pad, the aboral pleated skirt, the interambulacral areas, and the ambulacra. Each of these zones experiences plate insertion in the white areas and grows in the direction of the arrows, toward darker regions.

Chapter 3 - Helicoplacoids

Introduction

Early Cambrian helicoplacoids are fusiform to pyriform spirally pleated echinoderms (Figure 3.1), and perhaps the most disparate members of the Echinodermata. No other members of the phylum have developed a similar body plan, and few homologies connect helicoplacoids to other echinoderm groups. Since their discovery and original descriptions (Durham and Caster 1963, 1966; Durham, 1964), two papers describing new species have been published (Durham 1967, 1993) along with a dissertation chapter reinterpreting their morphology (Derstler 1985), and three recent papers have discussed their paleoecology and likely depositional environment (Bottjer *et al.* 2000; Dornbos and Bottjer 2000, 2001). The relationship of helicoplacoids to other early echinoderms has been discussed by several authors including Paul and Smith (1984), Smith (1988), Sprinkle (1992), Sumrall (1996), Mooi and David (1998), Dominguez-Alonzo (1999), and Mooi (2001), but there has been no consensus on where helicoplacoids fit in the echinoderm tree. This partly results from the drastically different body plan of helicoplacoids and the difficulty in discerning a suitable mode of growth. The most recent paper is currently in press by Sprinkle and Wilbur (2005), which discusses the bauplan and growth of helicoplacoids.

Helicoplacoids do not show the pentameral (modified radial) symmetry that is found in many other Cambrian and most later echinoderms. Furthermore, the body is wound into a left-handed spiral with no apparent body divisions other than ambulacral and interambulacral areas, and a possible attachment pad situated upon the lower pole.

Other Early Cambrian groups, including edrioasteroids and eocrinoids, have three zones of thecal plating with different types of growth, designated axial, perforate extraxial, and imperforate extraxial, each of which comprises equivalent portions of the skeleton (Mooi et al. 1994; Mooi and David 1998; Sprinkle and Guensburg 2001). Helicoplacoids show each of these skeletal regions, but vary greatly from other echinoderms in the contribution each makes to the overall theca. In particular, I propose helicoplacoids have a greatly reduced perforate extraxial region, which has made identification of orifices associated with waste removal and respiration difficult to identify. This body plan complicates discerning phylogenetic derivation considering the drastic modifications required of a generalized ancestral echinoderm bauplan to create the highly derived helicoplacoid test. Despite this, helicoplacoids unequivocally show echinoderm synapomorphies, including a water vascular system and plate stereom, and their ambulacral (axial skeleton) construction is similar to that of the earliest edrioasteroids (Paul and Smith 1984; Derstler 1985; Wilbur 2003).

History

The relatively recent discovery of helicoplacoids and the subsequent initial systematic work was carried out and published by Durham and Caster (1963). These authors established general morphologic patterns, and erected two new species, *Helicoplacus gilberti* and *Helicoplacus curtisi* to account for the perceived disparity encountered in the original available specimens. The theca is fusiform in shape, as long as 75 mm in height, and is composed of plated spiraling interambulacral pleats arranged in relation to what Durham and Caster interpreted as a single ambulacrum with one

branch. Each interambulacral pleat is capable of expansion through ratcheting of recumbent plates below the outermost plates. The mouth was interpreted by the authors to be at the more broadly curved end of the fusiform test, which was named the oral pole. The authors recognized no attachment structures or attached specimens, a conclusion that was supported by the apparent lack of clastic particles of size suitable for attachment, which led to the conclusion that these organisms were free-living.

This first work was followed up by Durham (1964) with an article written for Yale Scientific Magazine. Therein, Durham wrote of the need for further taxonomic work, citing the apparent existence of as many as four additional species. Durham also included an important omission from the first paper; that the plates are composed of stereom, allying the group with other echinoderms. Further study was conducted on the mode of contraction and expansion of the test, and the remainder of the paper was dedicated to the evolutionary significance of the group within the group Echinodermata (Durham, 1964).

A chapter written by Durham and Caster (1966) for the Treatise on Invertebrate Paleontology followed. The chapter did not add any new revelations on anatomy or systematics, but did suggest that helicoplacoids may represent a stem group retaining triradiate construction assumed to be ancestral in Echinodermata, which could be modified to the pentameral condition by addition of two additional ambulacra. Ambulacra were considered to be used solely for respiratory purposes, with feeding carried out by a proposed ciliated epidermis that served to collect food particles while in the expanded state, transporting them to the proposed mouth at the oral pole. Finally, while convinced that helicoplacoids were free-living, the authors entertained the

possibilities of a recumbent vagile epifaunal, upright sessile epifaunal, planktic, or nektic lifestyle (Durham and Caster, 1963).

Durham completed another paper on helicoplacoids in 1967, which was dedicated primarily to identification of new species and newly discovered morphologies. In particular, the ambulacral areas of a helicoplacoid were reconstructed. The amb was shown in cross section to have a medial ridge, with pore-bearing plates at either side of the base of the ridge. These pores allowed for passage of tube feet from an internal water vessel to the exterior, as in echinoids. The reconstruction was based largely upon a single specimen of the new genus and species *Waucobella nelsoni* Durham, 1967. In addition, Durham also named the new species *Helicoplacus everndeni*, *Helicoplacus firbyi*, and the new genus and species *Polyplacus kilmeri*, and reevaluated the previously named *Helicoplacus gilberti* and *Helicoplacus curtisi*. The new genera erected were for a unique specimen in one case, and for a single slab with two specimens in the other (Durham, 1967).

Derstler (1981) reevaluated helicoplacoids, and argued that the ambulacral areas protected by cover plates, implying that tube feet were internal to the amb, rather than external, as in the reconstructions of Durham (1967). Furthermore, Derstler asserted that the mouth lay at the junction of the ambulacral areas rather than at the pole, and that the animal was sessile, with the long axis perpendicular to the substrate upon which it lived (Derstler, 1981). These ideas were further developed in Derstler's dissertation (1985). He expanded on the idea that the organism was upright, suggesting that helicoplacoids were attached to skeletal debris by their lower pole, a conclusion based on a single equivocal specimen. Derstler also reinterpreted the ambulacral areas in accord with his

1981 paper, showing tube feet internal to the cover plate series, which would have afforded protection to soft tissues when closed. Interambulacral areas were interpreted as being fused and incapable of expansion and contraction, although Derstler did allow that the organism might have been able to bend slightly in a strong current (Derstler, 1985).

Derstler (1982) in an abstract argued that helicoplacoids were highly modified edrioasteroids. It is not explicitly stated whether he believed triradiate or pentameral symmetry represented the ancestral condition, but the abstract does clearly state that the helicoplacoids should be an order within Edrioasteroidea, and he suggested that two ambulacra were lost resulting in the triradiate condition. This proposed line of descent is in direct opposition to that of Durham (1967) who suggested that the ancestral echinoderm, whether or not it was a helicoplacoid, was likely triradiate.

Paul and Smith (1984) discussed helicoplacoids in a paper on the early radiation of echinoderms. The authors agreed with Derstler (1981) that the mouth lay at the junction of the ambulacral areas, and that ambulacra likely had a compliment of flooring and covering plates. A reconstructed cross section of the theca showed an amb similar to that of Derstler, but interambulacral areas that expanded between ridges through a series of small ratcheting plates. A phylogeny of the Echinodermata followed that showed solutans and helicoplacoids at the base of the echinoderm tree, in support of ancestral triradiate ambulacral arrangement (Paul and Smith, 1984).

Durham completed his final tome on the helicoplacoids in 1993, cementing his views on anatomy and the diversity of the group. Durham reasserted that the mouth lay at the upper ("oral" in his terminology) pole, contrary to the claims of Derstler (1981, 1985) and Paul and Smith (1984). Furthermore, Durham argued that helicoplacoids were

sessile, but instead of attaching to hard substrates, they were interpreted at having the more tapered of the two poles ("aboral" in Durham's terminology) inserted into soft substrates, anchoring the animal. The new genus *Westgardella* was erected for *Helicoplacus curtisi*, *Helicoplacus firbyi*, as well as the new species *Westgardella blancoensis*. In addition, Durham also named the new species *Helicoplacus casteri* and *Helicoplacus guthi*, bringing the total of named species to nine, making the helicoplacoids the most diverse Early Cambrian group of echinoderms (Durham, 1993).

Ambulacral morphology was considered an important diagnostic characteristic delineating the genera *Westgardella*, *Waucobella*, and *Helicoplacus*, while the ambulacra in *Polyplacus* are unknown. Durham made reconstructions of the ambulacra, showing clearly different ambulacra for each group, despite all sharing the same medial ambulacral ridge, lack of cover plates, and pores that would have exposed the tube feet along the flanks of the ambulacral ridge, in accord with his 1967 paper (Durham 1967, 1993).

Following Durham's systematic work, a trio of papers was published regarding the paleoecology of the helicoplacoids. The first (Bottjer et al., 2000) argued that the "Cambrian Substrate Revolution," caused the extinction of the helicoplacoids. The substrate revolution was a term introduced in this paper to summarize the widespread vertical bioturbation that originated during the Early Cambrian, disturbing bedding and microbial-bound substrates used by organisms as attachment surfaces. Helicoplacoids were considered sediment stickers, which anchored in soft substrates in accord with the interpretations by Durham (1967, 1993).

Dornbos and Bottjer (2000) focused on the sediment-water interface and the manner in which helicoplacoids interacted with the substrate. The authors argued that complete or nearly complete helicoplacoids were preserved in infrequent obrution deposits, which explains why frequently they are found recumbent upon a bedding surface overlain by graded beds. Two figured specimens were thought to represent cases of life-position preservation, with the lower pole imbedded perpendicular to bedding. The evolution of widespread infaunal organisms caused disturbed bedding and destruction of binding microbial mats, which then caused helicoplacoids to become extinct. Edrioasteroid and eocrinoid groups from the Early Cambrian escaped extinction, as these groups were capable of attaching to hard substrates, whereas Dornbos and Bottjer (2000) thought that helicoplacoids could not.

The final paper in the series (Dornbos and Bottjer, 2001) recounted the arguments made in the first two, and added that helicoplacoids were probably far more abundant than their fossil record indicates. The helicoplacoid theca was comprised of small skeletal plates held together by soft tissues is not conducive to preservation by anything less than large storms that deposit large amounts of sediment, burying specimens before decay and disarticulation. The well-preserved helicoplacoid bearing beds of eastern California, western Nevada, and eastern British Columbia represent an advantageous depositional window, while other helicoplacoid localities along the west coast of the North American continent show only isolated plates of completely disarticulated carcasses.

Occurrences

Helicoplacoids were first discovered in the siliciclastic lower member of the Lower Cambrian Poleta Formation of the Westgard Pass area of the White-Inyo Mountains of Inyo County, eastern California (Figure 3.2) (Durham and Caster, 1963). The most fruitful and therefore best-studied localities continue to be found in the 250 m (820 feet) of Poleta outcrop (Nelson, 1962) in this area. The formation is divided into two or three units by different authors, the only difference being that authors of the latter opinion consider an archaeocyath-bearing limestone at the top of the formation a separate member (Moore, 1976b; Signor and Mount, 1989). This chapter will follow the original division into two members and subsequent nomenclature devised by Nelson (1962). The lower member of the Poleta Formation is dominated by limestones, predominantly composed of thick bedded ooid shoals and archaeocyaths, some of which form reef structures (Nelson, 1962; Signor and Mount, 1989). The lower member has a minor amount of interbedded shale, in which are found the remains of another echinoderm, likely an edrioasteroid or eocrinoid, or possible both. These rocks represent the outer edge or upper outer slope of a carbonate bank environment, with terrigenous material originating from the southeast being deposited by tidal currents basinward of the bank (Moore, 1976a).

The upper unit is dominated by subtidal to intertidal siliciclastics, which can be broken down into five horizons; a lower siltstone, lower sandstone and siltstone, middle limestone, upper sandstone, and an upper limestone unit (Moore, 1976b), which again is designated a third member by some authors (Moore 1976a, 1976b). The lower siltstone

unit is composed of gray-green shales and siltstones at the base, thought to represent a subtidal mudbank. These rocks are separated from mudflat deposits up section by a limestone marker bed (Moore, 1976a). Minor limestone beds within the siltstones occur, some of which are composed primarily of helicoplacoid plate material (Durham, 1993). Helicoplacoids occur at the base of the lower siltstone member, which is best exposed at a dozen localities in the Westgard Pass area of the White-Inyo Mountains (Figure 3.3). While field guides, section descriptions, and geologic maps describe the helicoplacoid-bearing siliciclastic material as shale, it is metamorphosed in the White-Inyos, resulting in a phyllitic to schistose fabric that nonetheless does not overtly affect preservation, other than making a rock that more readily breaks upon foliation planes which are at an angle relative to bedding. The upper sandstone and siltstone unit is a 20 m (66 foot) thick wave-dominated bar complex, topped by a 30 m (98 foot) thick limestone and siltstone unit, representing a brief interval of carbonate bank deposition. This is topped by *Skolithos*-bearing quartzites deposited in the foreshore (Nelson, 1962; Moore 1976a, 1976b; Signor and Mount, 1989).

Helicoplacoids are found in association with the trilobite *Nevadella gracile*. This places them in the *Nevadella* zone, which is represented in the basal portion by the trilobite *Nevadia*, and at the top by the trilobite *Nevadella*. In the White-Inyo Mountains, this zone begins in the Montenegro Member of the Campito Formation, just below the base of the Poleta Formation. Here, the trilobite *Nevadia* is found, along with *Holmia* and several ichnotaxa. The zone extends up-section to the lower half of the helicoplacoid-bearing upper member of the Poleta, where *Nevadia* is replaced by the

trilobite *Nevadella* (Nelson, 1976). Helicoplacoids are found in the same beds as trilobite skeletal remains, the majority of which are comprised of molted cephalons.

Helicoplacoid-bearing Poleta Formation in the Montezuma Range occurs in adjacent Esmeralda County, Nevada, 6 miles west of the town of Goldfield, in Indian Springs Canyon (Figure 3.2). Stuart Hollingsworth (personal communication) is currently preparing a geologic map of the region at a 1:24,000 scale. The helicoplacoids collected at these localities are exceptionally well preserved; in some cased better so than at the type localities in the adjacent phyllitic siltstones of the White-Inyos. The Poleta Formation in the Montezuma Range is 579 m thick (1900 feet), 255 m (838 feet) of which accounts for the upper member (Albers and Stewart, 1972). Helicoplacoids were collected from three localities near the base of the upper member of the Poleta, two of which were collected extensively by the author (Figure 3.4). The formation at these localities is composed of a basal siltstone and phyllitic siltstone (Albers and Stewart, 1972), but the helicoplacoid-bearing rocks are far less metamorphosed than those encountered in the White-Inyos. The Indian Springs shales split along bedding planes while the White-Inyo phyllitic material splits along foliations more readily than the bedding plane. Here too, the helicoplacoid-bearing rocks occur below a limestone marker bed, which in the Indian Springs Canyon area occurs approximately 30 m (100 feet) above the base of the section (Hollingsworth, personal communication). Similar outcrop is encountered in the nearby Silver Peak area of Nevada, approximately 30 miles west of Goldfield, Nevada. Durham (1993) also included specimens from this locality, some of which were restudied herein.

The relative abundance of articulated helicoplacoid specimens in the Poleta Formation and paucity of complete specimens elsewhere was one topic covered by Dornbos and Bottjer (2000; 2001). Complete or relatively complete specimens are found along bedding planes at the base of graded beds, suggesting that these specimens were buried rapidly (Dornbos and Bottjer, 2000; 2001). Helicoplacoid preservational potential was likened to that of asteroids, ophiuroids, eocrinoids, and edrioasteroids, which have plates of skeletal tissue that are loosely held together by ligaments and musculature (Durham, 1993; Brett et al., 1997). As helicoplacoids died, the tissues responsible for shape maintenance degraded, probably in a matter of days (Dornbos and Bottjer, 2001), leaving disarticulated plate material to cover bedding planes, and in some cases, to comprise small (40 cm thick) grainstone lenses (Durham, 1993). It was concluded that helicoplacoids were widespread, but well-preserved specimens that entered the fossil record lived in very low energy environments that were beset by intermittent storm-driven obrution deposits which rapidly buried the organisms (Dornbos and Bottjer, 2001).

The conclusion that helicoplacoids were more widespread than the record of complete specimens may indicate is supported by occurrences in eastern Washington, eastern British Columbia, Canada (Sprinkle, 1976, Durham, 1993), and northwestern Mexico (Durham, 1978; James W. Hagadorn, personal communication) (Figure 3.2).

The Addy Quartzite of Addy, Stevens County, eastern Washington (Figure 3.2), yields disarticulated helicoplacoid plates (Durham, 1978, 1993) that, while not as abundant as at White-Inyo localities, nonetheless can be found commonly scattered across bedding planes. Okulitch (1951) first described the Early Cambrian fauna at the locality, which is now recognized as containing helicoplacoid plates. The locality was

described as occurring on the southern end of a ridge immediately adjacent to the town of Addy, on the western bank of the Colville River (Figure 3.5). The physical stratigraphy was difficult to interpret as the outcrop occurs on fault-bounded exposures (Lindsey et al., 1990, Miller, 1996), making definite stratigraphic assignment impossible (Lindsey et al., 1990). The predominant lithology within the outcrop studied by Okulitch is a white- and gray medium grained quartzite interbedded with a fossiliferous argillite and siltstones (Miller, 1996). Other fossils found include hyoliths, brachiopods, and the trilobite named *Nevadia addyensis* by Okulitch (1951), later renamed *Nevadella addyensis* (Lindsey et al., 1990), which places these rocks firmly within the *Nevadella* trilobite zone (Nelson, 1976). The presence of helicoplacoid debris within siltstones supports both conclusions of Dornbos and Bottjer (2000, 2001), namely that helicoplacoids were found in a variety of environments, and that preservation is inhibited in higher energy environments without obrution deposits.

Another helicoplacoid locality occurs further north in the Solitude Range, Rodgers Pass/Big Bend region, British Columbia, Canada, along the margin of the Laurentia paleocontinent (Figure 3.2). The rocks in this region were first studied in the summers of 1959-1961 by using helicopter to investigate outcrops that occurs above tree line (Wheeler, 1962). Atop a ridge bounded by the confluence of the Columbia and Sullivan Rivers, at a locality described as "100-200 yards east of the headwaters of Boulder Creek" (Jean Dougherty, personal communication). J. F. Ricker, a field assistant of J. O. Wheeler, collected a rock that contained unidentified fossils that occurred with trilobites misidentified as *Olenellus* (Wheeler, 1962). The trilobites were later rediagnosed as *Nevadella eucharis*, placing the fossils within the Early Cambrian

Nevadella zone. The unidentified fossils were later recognized as helicoplacoids, but the problems presented by field collecting for mapping purposes and transport by helicopter, only two or three disarticulated specimens were collected (Durham, 1993). These specimens were borrowed from the Geological Survey of Canada (GSC) and photographed by Durham for the preparation of his 1993 manuscript. The author attempted to borrow these same specimens, but Jean Doughtery of the Geological Survey of Canada found only a note in their place indicating that the specimens were borrowed by Durham (personal communication), who passed away before he had the opportunity to return the helicoplacoids. A search of the University of California Museum of Paleontology failed to unearth the specimens, or the photographs taken of them; the only physical evidence available to the author of the existence of these fossils is a single photograph of the lower pole of a single specimen published in Durham (1993; figure 5-7).

The helicoplacoid from the Solitude Range was "badly jumbled" in Durham's words (Durham, 1993), but would by examination of the photograph fit into Taphonomic Group Two of Dornbos and Bottjer (2001) (see section on taphonomy), indicating some but not complete degradation of soft tissues before burial. This suggests the likelihood of the same preservational potential as existed in coeval deposits in the White-Inyos, which in turn indicates that well-preserved helicoplacoids occur in the Canadian Rockies. With this in mind, the author attempted in the summer of 2003 to scale the aforementioned ridge visited 43 years before, and found it as necessary now as in 1960 to visit the locality by helicopter.

The Canadian material was erroneously reported to be from a locality in Northwestern Alberta in Durham's 1964 paper (Durham, 1993), an error that has reappeared in some subsequent publications on the group (e.g., Durham, 1967).

The final unconfirmed report of helicoplacoid material is of an occurrence in northwestern Sonora, Mexico in Early Cambrian strata (James W. Hagadorn, personal communication). The locality has not been visited by nor revealed to the author, but is probably within the vicinity of a well-known Late Paleozoic to Early Cambrian section in the Proveedora Hills (Figure 3.2) (e.g. Sprinkle, 1973; Fritz, 1975).

Helicoplacoid occurrences worldwide are confined to western North America, but there are many more localities that produce helicoplacoid material that are now known versus the range known to Durham and Caster (1963). Their distribution was along nearly the entirely of the East-West trending northern coast of Early Cambrian Laurentia (Scotese, 1988), with a far more widespread range than originally understood (Durham and Caster, 1963; Dornbos and Bottjer, 2000, 2001).

Localities

Helicoplacoids were collected by the author at 10 localities in the White-Inyo Mountains of East-Central California, localities in the Indian Springs area of West-Central Nevada, and one locality in the town of Addy, Northeastern Washington. For further locality information, including latitude and longitude, age, zonation, and associated faunas, see the tables in the introductory chapter.

Taphonomy

Helicoplacoid taphonomy and the resulting geographical distribution of helicoplacoid faunas were covered in great detail in Dornbos and Bottjer, 2001; the following is a short summary of their findings.

Helicoplacoids are only very rarely preserved intact or partially intact. This is because of the construction of helicoplacoids specifically, and echinoderms in general. All echinoderms have some contribution of spongy skeletal tissue and mutable collagenous tissue making up the body wall (Wilkie and Emson, 1988). Holothurians have greatly reduced skeletal ossicles and a predominance of mutable collagenous tissues, while echinoids have a test composed of broad tightly sutured skeletal ossicles and very little mutable collagenous tissue. The evolutionary advantage conferred to holothurians by this strategy is greater flexibility to the test, while echinoids have a test more resistant to predation. Asteroids, fossil crinoids, and ophiuroids have bodies composed of nearly equal contributions of mutable collagenous tissues and skeletal ossicles, somewhere in-between the spectral endpoints of holothurians and echinoids. Brett et al. (1997) conducted a study on echinoderm taphonomy that created categories for particular echinoderm taphonomic types, according to suturing of the skeletal ossicles and the prevalence of soft tissues in binding the skeleton. Type one echinoderms are those with skeletal ossicles bound by ligaments or musculature, or loose skeletal ossicles in a matrix of soft tissues. This group includes ophiuroids, asteroids, paleoechinoids, eocrinoids, and edrioasteroids. These animals are only rarely preserved as entire body fossils, and are more commonly preserved as single plate elements. Type two echinoderms include those with portions of the skeleton that are tightly sutured, and

portions that are less well bound. Crinoids, regular echinoids, and cystoids fit into this group, with crinoid and cystoid arms and echinoid spines being the less-well sutured body parts. These echinoderms are more likely to have the theca preserved, stripped of all appendages. Type three echinoderms include those with skeletal ossicles so tightly sutured that the theca is more likely to break across a plate face than across a suture. This group includes camerate and microcrinoids, blastoids, and irregular echinoids. These are most commonly preserved as entire thecas or tests, with complete specimens preserved far more commonly than is found in group two (Brett et al., 1997)

The timing of decay and disarticulation is the driving factor behind such an analysis. Field studies of echinoids in a low energy back-reef environment indicate that soft tissues completely disappear by six days after the death of the animal (Greenstien, 1991). Crinoids and ophiuroids become completely disarticulated in reef flat tide pool environments (Meyer, 1971), whereas crinoids in higher energy disturbed environments disarticulate in as rapidly as 2 days (Liddell, 1975). Asteroids begin to decompose and fill with decompositional gasses three days after death, soft tissues begin to lift away from skeletal tissues 6 days after death, and completely disappear after 11 days. Complete disarticulation of asteroid tests comes 17 days after death (Schafer, 1972; Donovan, 1991). Liddell (1975) found that rapid burial of recently dead specimens greatly improves the chance of preservation, as specimens exhumed six days after burial remained articulated and retained pigmentation in the soft tissues, usually the first sign of decomposition. This gives echinoderms between 0 and 6 days after death for burial to be completely preserved, or from between 6-17 days to be at least partially preserved.

Helicoplacoids belong in the type one taphonomic class (Brett et al. 1997), as the skeletal ossicles making up the theca are not tightly sutured, but rather held together entirely by soft tissues (Durham, 1993; Dornbos and Bottjer, 2001). Furthermore, Dornbos and Bottjer (2001) found that there is no particular body region that is more resistant to decay than any other.

In order to classify the types of preservation commonly found in helicoplacoids, Dornbos and Bottjer (2001) devised an index of helicoplacoid preservational types. The first includes well-preserved specimens with slight disarticulation; the second includes partially disarticulated specimens, and the third "almost fully disarticulated specimens" (Figure 3.6). This index coupled with that of Brett et al. (1997) indicates that those specimens encountered in index one were probably killed by the act of entombment. Group two helicoplacoids were probably killed by storm surges, allowed to decay for anywhere from one to two weeks before a second storm system suspended enough sediment to bury the remainder of the carcasses, or were buried and decayed some degree post-entombment (Dornbos and Bottjer, 2001). Group three helicoplacoids represent those that died under normal conditions and were rendered to free skeletal ossicles covering bedding planes long before the arrival of storms. Specimens studied by Dornbos and Bottjer (2001) show that at a single locality within the White-Inyo Mountains, 19% of specimens were categorized as group one, 69% were categorized as group 2, and 12% were categorized as group 3.

Inferred obrution deposits in normally low-energy regimes were concluded to be the most likely culprit in the preservation of Taphonomic Group One and Taphonomic Group Two helicoplacoids. Dornbos and Bottjer (2001) examined X-radiographs of

sedimentary cores that indicate little to no bioturbation, and graded bedding. These two factors indicate a shallow redox boundary just below the sedimentary surface, and periodic large influx of sediment, respectively. Together, these explain the abundance of type two helicoplacoids, which are presumed to have been killed just before burial, or buried and then slightly decayed in anoxic sediments (Dornbos and Bottjer, 2001).

Furthermore, the presence of helicoplacoids in the fine-grained siliciclastics of the upper Poleta Formation represents a "taphonomic window" of preservational opportunity. The authors argued that helicoplacoids were more widespread, but are only preserved in the sediment type and environmental conditions that produced the upper member of the Poleta Formation (Dornbos and Bottjer, 2001). This premise is supported by the occurrence of completely disarticulated helicoplacoid debris in the coarser grained siltstones of the Addy Quartzite in northeastern Washington. It is apparent that helicoplacoids existed along the entire northern coast of Early Cambrian Laurentia (western North America) and was only preserved in low energy environments that were periodically subject to large tropical storms resulting from the tropical position of Laurentia at that time.

Materials and Methods

Helicoplacoids, like all echinoderms, have a skeleton composed of monocrystalline high-Mg calcite, which is frequently dissolved or replaced by other minerals; in the Indian Springs region of western Nevada, helicoplacoid plates have been replaced by kaolinite (Loren Babcock, personal communication). The vast majority of all

helicoplacoids collected have had their plates dissolved, preserving the fossils as natural molds.

Some minor preparatory work was carried out upon fossils collected by the author and deposited in the Texas Memorial Museum. Infrequently, White-Inyo specimens retain carbonate plate material. These fossils were prepared by repeatedly administering a 10% HCl solution, which slowly etched the plates, then thoroughly rinsed. The natural molds were then wetted, and filled with a solution of "Mold Builder" liquid latex rubber, manufactured by Environmental Technology Incorporated of Fields Landing, California, mixed with black powder tempera, manufactured by Palmer Show Card Paint Company of Troy, Michigan. Upon drying, which takes on average three days depending on thickness of latex applied and humidity, the latex is slowly peeled away, resulting in a blackened latex positive of the moldic fossil. These are then "smoked," by applying an ammonium chloride sublimate that whitens the higher relief of the fossils, leaving the crevasses darkened, highlighting contrasts.

This process is for the most part non-destructive. The blackened latex can in some cases leave a stain where the latex was applied to the rock. Derstler wrote (1985) that stains could be avoided if the tempera-latex solution were allowed a "month or so" before being used to cast specimens, but the author experienced no such diminishment in staining. The most serious consequence is the excavation of the more friable helicoplacoid steinkern that is retained in some specimens. In some cases, however, casting can be considered a type of preparatory technique, because if removal of the internal mold is required, successive castings remove successively more of the rock. This is destructive, but in carrying out serial castings, the internal anatomy can be analyzed

while gradually revealing the external anatomy on the side opposite the steinkern. With care, including wetting the surface of the rock while the latex cast is being removed, steinkern removal can be avoided altogether.

Museum specimens studied herein were cast using uncolored latex, in order to avoid the aforementioned stains. The latex casts were darkened in the laboratory by painting them with waterproof black India ink. The resulting smoked casts show nearly the same quality of fine details as the blackened latex casts. The one failing of this method occurs when ink is too liberally applied, resulting in cracks upon drying of the coat.

Specimens Studied

Many different museum collections were accessed in preparation of this dissertation. Silicone casts of the original type collections were graciously donated to the Texas Memorial Museum (TMM) by the University of California Museum of Paleontology (UCMP) through the efforts of Dave Haasl, as well as loans of latex casts of many types and non-types, including in some cases the original latex casts studied by J. Wyatt Durham. The recently accessioned collection of helicoplacoids used for the preparation of Bottjer et al., 1999, and Dornbos and Bottjer, 2000, and 2001 was accessed at the Los Angeles County Museum of Invertebrate Paleontology branch of the Los Angeles Natural History Museum (LACMNH), with the aid of Steven Q. Dornbos of the University of Southern California and Harry Filkhorn of the LACMIP. The collections made by N. B. McCulloch in the summer of 1967 for the United States National Museum (USNM) were accessed, with the aid of Daniel Levin and Jan Thompson. Two additional

specimens were cast at the North Museum at Franklin and Marshall College (NM) while studying *Camptostroma* specimens, with the aid of Jon Coolidge III and Alison Eichelberger.

Ed Fowler of Palmdale, California graciously donated several specimens to the Texas Memorial Museum, and Dr. Richard Squires of California State University at Northridge furnished an additional cast of a particularly gregarious group of helicoplacoids. Helicoplacoid material was collected in 2003 by the author from Addy Quartzite outcrop in Addy, Washington, on the property of Northwest Alloys, Incorporated, with the permission of Calvin Davis. A collection made by Dr. James Sprinkle of the University of Texas in the 1976 and 1982 field seasons and was accessed. The author also amassed a collection of helicoplacoids, from the White-Inyo Mountains of east-central California during the field seasons of 2001-2004, and from the Indian Springs area of west-central Nevada during the field seasons of 2002-2004. These specimens are to be accessioned by the Texas Memorial Museum upon completion of this dissertation.

Morphology

Helicoplacoids are bulb- ("inverted pear" [Sprinkle and Wilbur, 2005) to spindle-shaped ("rugby ball shaped" [Dominguez-Alonso, 1998]) echinoderms, the largest of which reach about 50 mm in height. The organism was oriented with its long axis perpendicular to the seafloor, with the more tapered end serving as a suction pad for attachment to hard or semi-lithified substrates (Wilbur, 2004). The theca was composed of rows of elongate interambulacral pleats, which were arranged in a left-handed spiral

upon the entire surface of the animal. The mouth of the animal was mediolateral, with three ambulacra situated between interambulacral areas, radiating away from the mouth (Derstler, 1981, 1985; Paul and Smith, 1984; Dominguez-Alonso, 1998). One ambulacrum spirals toward the lower pole, while the other two spiral toward the free upper pole (Figure 3.1).

Helicoplacoids are the most disparate of the Early Cambrian echinoderms. The pentameral ambulacral symmetry that is nearly ubiquitous in the Echinodermata save for a few cases (the "carpoids" and a few highly derived blastozoans) is reduced in helicoplacoids to a triradiate ambulacral system. Furthermore, the radial symmetry imposed upon the theca of the helicoplacoids is independent of the junction of the ambulacral areas; in other echinoderms the mouth is along the axis of symmetry. The spindle-shaped theca is also unique in the echinoderms, as is the unique system of ratcheting plates responsible for contraction and expansion of the test.

The Extraxial-Axial Theory (Mooi et al., 1994; Mooi and David 1997, 1998; David and Mooi, 1998) was devised from a developmental standpoint for understanding echinoderm skeletal homologies. The body of every echinoderm can be partitioned into homologous regions as discerned through developmental and fossil data; the Axial Region (AR), Perforate Extraxial Region (PER), and Imperforate extraxial region (IER). Recognition of each of these regions is more difficult in the highly derived helicoplacoids as opposed to a more generalized echinoderm, such as *Camptostroma*, but reasonable assignments of each of these skeletal regions can be made, indicating growth and development of the helicoplacoid bauplan. Helicoplacoids were included in a general comment on the nature of the earliest echinoderms, suggesting that these primitive

animals had a skeleton composed of nearly equal percentages all three systems (Mooi et al., 1994). This argument exaggerated the relative contributions of each region, but was nonetheless correct in recognition of each region, which was overlooked by Sprinkle and Wilbur (2005), where it was thought that the Imperforate extraxial region was probably lost.

Axial region

The Axial region of all echinoderms is the portion of the skeleton dedicated to support of the water vascular system. This includes the mouth, peristomal plates; podial pores, brachiolar plates and brachiolar cover plates, ocular plates, and ambulacral floor plates and cover plates.

Growth of axial skeletal elements originates at the terminal or ocular plates radially oriented around a primordial mouth frame; skeletal elements increase in size after insertion at the ocular plate, resulting in narrower (younger) ambulacral plates away from the mouth (Mooi et al., 1994). Helicoplacoids lack brachioles and therefore brachiolar plates, but do show all other anatomical features. The primary difference in the ambulacra is in their number. Helicoplacoids have a triradially-arranged ambulacrum, as opposed to the pentameral ambulacral symmetry that is more common in other echinoderm groups. From a mediolateral confluence of the three ambulacra, two spiral toward the upper pole, separated by one to three (usually two) interambulacral ridges. In adults, the lower of the two upper ambulacra extends for one half of the circumference of the animal, terminating approximately opposite the mouth. The upper of the two ambulacra continues for one full circumference, terminating far before reaching the upper

pole. There are usually 10 interambulacra separating the mouth from the uppermost ambulacrum. A third ambulacrum spirals downward toward the lower pole, completing about 1.5 revolutions before terminating well before reaching the lower pole. There are anywhere between 8-12 interambulacra separating the mouth from the lower amb.

It was originally asserted by Durham and Caster (1963, 1966) and Durham (1964, 1967), and reasserted by Durham (1993) that the mouth of helicoplacoids lay at the apex of the animal, the point furthest from the substrate, which was named the "oral pole." It was proposed that a ciliated epidermis carried out food collection over the entire surface of the theca. Settling particles were collected in the interambulacral grooves, which transported them toward the upper pole and the "mouth" (Durham and Caster, 1963). The ambulacra and tube feet were thought to be relegated to respiratory function (Durham, 1993).

Derstler (1981, 1985) and Paul and Smith (1984) argued, contrary to the assertions of Durham that the mouth lay at the junction of the ambulacra rather than at the upper pole, a notion subscribed to here for three reasons. First, ambulacra and the tube feet contained within are used for feeding in most other echinoderm groups, and in all other Early Cambrian groups. *Camptostroma* and *Stromatocystites* in fact have no possible feeding alternative. Second, the ambulacra in adult helicoplacoids fail to reach the upper pole (Paul and Smith, 1984), except for in the questionable case of a single incomplete specimen of *Waucobella nelsoni* Durham 1967. What was interpreted as an "oral pole" is merely a poleward end of an incomplete test. This fossil shows evidence of tapering at the ambulacral terminus, but no terminal whorl exists to unequivocally establish that the ambulacral termination occurred at the pole. The upper ambulacrum

reaches the upper pole, but only in the case of some juveniles. As feeding is required at all stages of life, this could not have served as the mouth. Furthermore, the spindle shape of the test of *Waucobella* suggests that it may be a juvenile. The implications of this ambulacral morphology for growth will be discussed later. Third, all other Early Cambrian echinoderms, and all extant groups, with the exception of some irregular echinoids, have a mouth that occurs at the termination of the ambulacral areas, a product of the evolutionary history of ambulacra as food-gathering structures and facilitation of growth (see section on growth). For these reasons, the mouth almost certainly occurred at the mediolateral ambulacral junction.

The mouth lies between 63% and 77% of the total height of the animal, and is close to the plane that passes through the widest portion of the test. The oral cover plates are poorly known as only a few helicoplacoid specimens retain a full complement of covering plates surrounding the mouth, much less the mouth itself. Oral and ambulacral plates appear to have been a zone of weakness along which many nearly articulated specimens are ripped open. Additionally, the small plates surrounding the mouth are subject to the biases against small skeletal elements and the rapid decay of flesh common to all echinoderms (Donovan, 1991). The few preserved oral areas of helicoplacoids show cover plates virtually identical to those seen in the ambulacral areas, which suggests the oral cover plates were not fused as is the case in some edrioasteroids, but could be "opened," a conclusion also proposed by Derstler (1985).

Oral cover plates show the same pattern of tessellate plates as the ambulacra do, with the addition of one additional row of small plates along the distal tips of the oral cover plates immediately above the mouth, which likely accommodated for the extra

surface area resulting from the gap at the point of ambulacral juncture. Only a single specimen shows evidence of a primary ambulacral plate, similar to those found roofing the mouths of edrioasteroids (Bell, 1977) (Figure 3.7). Considering there is only a single plate in this region, below the mouth, it is probable that this represents the right primary ambulacral plate, supporting the premise that the down-going ambulacrum is in fact A. There are no other primary ambulacral plates visible, but the presence of a single primary ambulacral plate suggests fused oral cover plates, that were incapable of opening.

The oral interior is known only from a specimen figured by Derstler (1985) and a few badly jumbled specimens collected by the author; the interior is even less commonly preserved than the oral cover plates. The only drastic difference in the oral floor plates versus ambulacral floor plates is the apparent lack of pores between adjoining plates (Derstler, 1985). This is difficult to conclude based on a single specimen, but until more specimens bearing internal oral areas are collected, the interpretation stands.

Durham (1967) created the first reconstructions of the ambulacral areas of helicoplacoids. The exceptionally preserved ambulacrum of *Waucobella nelsoni* Durham 1967 served as the model of the helicoplacoid ambulacrum, which included the interpreted lack of a flooring plate series (Figure 3.8). The cover plate series in this specimen is relatively complete, but the ambulacrum itself is dislocated from the interambulacral rows within which it was imbedded, exposing a proximal row of plates that have the cross-sectional profile of an I-Beam. When aligned in series, these indented "I-Beam" plates abut in a manner that conjoins the indentations, creating a single large dish-shaped indentation between successive plates. Durham (1967, 1993) interpreted these plates as the basal cover plates, and concluded that the indentations were pores that

allowed passage of tube feet from internal ampullae through the amb onto the exterior of the theca.

Inherent to this interpretation is an ambulacrum with a central ridge flanked by tube feet that were perpetually exposed to the external environment, similar to the tube feet of modern echinoids. Further ambulacral reconstructions followed for two newly erected genera (Durham, 1993) showing a similar pattern of proximal cover plates with pores in orientations that varied depending on the genera. *Waucobella* showed pores between successive proximal plates, and at least five distal series of plates. *Helicoplacus* showed similar pores between successive plates, but only three distal series of plates. *Westgardella* showed pores between two adjacent proximal series of plates, a basal series of cover plates sans pores, and three distal series of cover plates with a different arrangement (Figure 3.9) (Durham, 1993).

Paul and Smith (1984) and Derstler (1985) followed Durham's work with plating models suggestive of the ambulacra in the Cambrian taxa *Stromatocystites* and *Camptostroma*. Ambulacra had biserially arranged floor plates with pores between adjacent plates, roofed over by three rows of ambulacral cover plates. This model is for the most part accurate, despite Durham's (1993) insistence to the contrary. Durham's inaccuracy stemmed from misidentification of the floor plates in the type specimen of *Waucobella*, which were taken to be the proximal row of "cover plates." The amb in this specimen was distended during compaction, exposing the floor plates. Durham took this as evidence for a lack of flooring plates and tube feet that perforated the covering plates. The "pore for tube foot" identified by Durham in a second genus, *Helicoplacus*, is an indentation at the point of articulation between the basal portion of a cover plate and the

immediately underlying floor plate. This pit was the attachment point for a ligament that aided in the closure of the cover plate series, similar to that of edrioasteroids (Figure 3.10) (Smith, 1985).

Durham identified an internal view of an ambulacrum (Durham, 1993; Figure 5-4) as the junction of one row of cover plates and one row of floor plates. This structure does indeed show an internal view of an ambulacrum, but the pores lie between floor plates, which Durham misidentified as the base of the cover plate series (Figure 3.11).

Ambulacral areas were composed of biserially arranged flooring plates, with sutural gaps that formed pits between adjacent flooring plates. Flooring plates are larger nearer the mouth and smaller distally (Figure 3.12), indicating that growth occurred at the tips of each ambulacrum, in accord with the Ocular Plate Rule of Mooi and David (1997). The sutural pores between plates did not necessarily pass through the floor of the ambulacrum into the interior of the theca, as in the ambulacral models created for helicoplacoids by Durham (1967) and for edrioasteroids by Bell (1976). The radial water vessel likely laid in the interior of the ambulacral groove between the flooring plates of the ambulacrum, with biserial outpockets of the water vascular system for the ampullae and tube feet (Figure 3.13). The base of the ampullae rested in the sutural pores between amb flooring plates, similar to the reconstruction by Paul and Smith (1984). Unlike this reconstruction, which shows a tube foot firmly sutured to the interior of the cover plate sheet, tube feet were used for feeding and respiratory purposes, along with opening of the cover plate series. This may have been accomplished by a secondary compensation sac, or more likely by inflation of the ampullae or tube feet themselves. Food was collected and passed along the amb to the mediolateral mouth.

Helicoplacoid cover plate series are almost identical to those found in edrioasteroid taxa, and are almost certainly homologous structures. The terminology devised by Smith (1985) is suitable for the discussion of helicoplacoid ambulacra. Helicoplacoid cover plate series were composed of a sheet of tessellating plates. The proximal primary cover plates are wide hexagonal plates that articulate in a 1:1 ratio with a corresponding flooring plate. These articulate with a row of smaller secondary cover plates, of which there are two types. Wide plates in the shape of a right pentagon articulate with the distal edges of the primaries, and elongate hexagonal plates lie in a gap between these pentagonal secondaries (Figures 3.10, 3.14). A tertiary row of small polygonal plates lies at the tips of the secondaries in the oral region. These plates are only preserved in rare cases (Figure 3.10); a specimen figured by Paul and Smith (1984) (Figure 3.15) shows these plates, as does *Waucobella nelsoni*.

These plates were not tightly sutured to the remainder of the amb, which in conjunction with the bias against small skeletal elements in the fossil record, contribute to this plate row being poorly represented in the record of the helicoplacoids. Ambulacral plates as well are larger near the mouth and smaller away from the mouth, suggesting growth mediated by the Ocular Plate Rule (Mooi and David, 1997). The ocular plate moderates the coincident growth of alternating flooring plates and covering plate sheets, ensuring that all elements grow in concert. Both the flooring and covering plates grow disproportionately, increasing in width (along the axis of the amb) more readily than in length (perpendicular to the axis of the amb).

Helicoplacoid ambulacra are flanked by interambulacral columns, or more accurately by the accessory plates of the interambulacral column. Interambulacra are

constructed of a medial ridge, with flanking accessory plates that ratcheted underneath (see discussion of interambulacral columns). It is these accessory plates that articulated directly with the amb. On the contrary, Derstler (1985) argued that the "northern" (upper-poleward) amb floor plates articulated with an interambulacral ridge plate, while the "southern" floor plates articulated with IA accessory plates. Several specimens of expanded helicoplacoids reveal the accessory plates in relation to helicoplacoid ambulacra and support the author's conclusions.

Assignment of helicoplacoid ambulacra according to the Carpenter system of notation (Carpenter, 1884; Ubaghs, 1968a) is dependent on the identification of other structures associated with the echinoderm test, such as the hydropore, gonopore, and anal pyramid of the Perforate extraxial region, none of which have been found in helicoplacoid echinoderms. There does exist a single plane of symmetry involving the ambulacrum that bisects the mouth and the amb that spirals toward the lower pole. The lower amb is therefore "A," making the other ambulacra B or C, and D or E respectively. Paul and Smith (1984) and Derstler (1985) both label the ambulacra as "B/C" and "D/E," while suggesting that helicoplacoids show ancestral triradiate ambulacral morphology. For reasons discussed in the forthcoming section entitled "Evolutionary Relationships" I believe the remaining ambulacra to be B and D, C and E having been lost during evolution of the spiraling helicoplacoid theca. Inherent to this argument is that the ancestral echinodermal condition was a 2-1-2 (Sprinkle, 1973) variant of the familiar pentameral ambulacral arrangement, that helicoplacoids show ambulacral reduction, and that helicoplacoids are highly derived, not ancestral (Sprinkle and Wilbur, 2005).

Perforate Extraxial

The perforate extraxial region is the perforated coelom-enclosing portion of the skeleton. The perforations allow for communication of coelomic tissues with the external environment; most of the thecal surface area dedicated to these purposes is used for respiratory purposes. This skeletal system also includes the skeletal structures dedicated to the support of the hydropore, gonopore, and anus (Mooi and David, 1997).

These structures have yet to be identified in the helicoplacoid test, despite an avid search by the author, as well as all previous workers. This suggests that these orifices are found within a greatly reduced perforate axial region. These orifices must of course exist in any echinoderm; in helicoplacoids the most likely places for these openings are at the lower or upper pole. The following section on the imperforate extraxial region discusses attachment at the lower pole, leaving the upper pole as the only likely candidate for position of the anus, hydropore, and gonopore, and also sequestration on the perforate extraxial region. This pattern is also seen in modern echinoids, which have a perforate extraxial region reduced to a small disc containing the ocular plates, periproct (anus), genital plates, and hydropore, all of which are in relatively close contact (Mooi et al., 1998). While echinoids have distinct skeletal elements dedicated to each of these orifices, they are derived from a more general echinoderm bauplan that had all three skeletal regions equally represented. The difficulty in recognizing the orifices within helicoplacoids may be a consequence of their position so early in the record. Echinoderm ancestors that gave rise to helicoplacoids may not have developed heavily skeletized structures associated with body orifices, such as a valvular anal pyramid or a plate-like madreporite by the time helicoplacoids arose. Contemporary echinoderms show only

evidence of an anal pyramid, which shows that these ossified skeletal elements were not ubiquitous until later in the echinoderm record.

Imperforate Extraxial Region: Interambulacral Areas

Intuition would indicate that the interambulacral areas of helicoplacoids are derived from the perforate extraxial region, as they are in other echinoderm groups (see sections on *Gogia*, *Stromatocystites*, and *Camptostroma* herein). However, there are many problems with this interpretation that can be resolved by assignment of the interambulacral areas to the imperforate extraxial region. These problems and their subsequent resolutions follow.

Helicoplacoid interambulacral areas are comprised of a series of helically arranged pleated interambulacral plates. Each pleat has a series of thick, rounded or inverted V-shaped, medial plates that protrude above the test surface, sometimes with ridges or short spines, accompanied by two grooved ("taco-shaped") lateral plates, one toward the lower pole, and one toward the upper. Derstler (1985) named the medial plates "ridge plates" and the recumbent plates were named "accessory plates;" that convention will be followed herein. The accessory plates were hinged between pleats and were capable of ratcheting outward to expand the test (Figure 3.16) (Durham and Caster 1963; Durham 1967; Derstler, 1985); however, the interambulacral models reconstructed by previous authors do not correctly show how expansion and contraction were accomplished.

Paul and Smith (1984) reconstructed interambulacra with an expansion zone, explaining that helicoplacoids could change shape, but not volume. The cross section of

the expansion zone shows accessory plates that are flattened and are therefore inaccurate, and also show seven highly organized rows of tiny plates in-between the accessory plates. The specimen studied as well as a few other large specimens show these same tiny skeletal elements imbedded in the areas between accessory plates. It was originally assumed by the author that this was sediment imbedded in the pleats during burial; however on closer examination there is structure to the arrangement of the skeletal elements, and the "particle" size is much greater than that seen in the surrounding rock. These probably represent vestigial skeletal remnants that became reduced in order to favor flesh and flexibility. The vestigial skeletal plates are only manifest in mature specimens with a long growth history.

Derstler (1985) showed an interambulacrum with fused accessory plates, and wrote that it was possible that helicoplacoids may have been able to twist or bend in response to currents, but were unable to change the volume of the theca. Considering the energetics of the paleoenvironment that helicoplacoids lived in, it is unlikely they had to contend with any currents at all, other than those associated with the infrequent obrution deposits that, as shown by their burial, helicoplacoids were unable to cope with.

Durham and Caster (1993, 1966) and Durham (1964) reconstructed an expanding interambulacral column, with a ridge and accompanying accessory plates. Durham (1993) mentioned that a specimen was sectioned in preparation of the reconstruction; it is apparent that the specimen in question was retracted, as the reconstruction of a retracted helicoplacoid shows crushed plates relatively jumbled under the overlying ridge plates. Also, the reconstructed accessory plates are misshapen; in specimens examined by the author, accessory plates have slight curvature, with the concave side outward when

expanded. When retracted, the concavities of accessory pleats occluded. Accessory plates were attached to one another proximally at their bases, and distally to the ridge plates (Figure 3.16).

Ridge plates are wide, with flat edges and a "V" shape in cross section, with the vertex distal. Rows of ridge plates were connected to one along their lateral faces, and to the adjoining accessory plates by ligaments or other soft tissues along the proximal edges of the plates. As plates are not sutured, and plate sheets are often distended during burial, it is most likely that the interambulacral columns were held together with soft tissues and ligaments, which again account for the ease with which helicoplacoids were disarticulated. The soft tissues in specific were most probably mutable collagenous tissues (Wilkie and Emson, 1988) ubiquitous to the echinoderms, which would account for the great thecal flexibility seen in fossilized specimens.

Helicoplacoids expansion has been debated between the groups of helicoplacoid authors. Durham and Caster first asserted that helicoplacoids were capable of accordion-like expansion, and further asserted these claims in Durham, 1964, Durham and Caster, 1966, Durham 1967, and Durham 1993. Paul and Smith (1984) wrote that helicoplacoids were capable of shape change but not volume change, by expansion of zones of small plating between interambulacral accessory plates. Derstler (1985) asserted that helicoplacoids could not have changed in volume, but were pliable to the point of minor shape changes because of strong currents. The unique interambulacral construction, preservation of fossils that clearly show expanded or contracted states, and coordination of ambulacral areas with interambulacral areas overwhelmingly support that

helicoplacoids were capable of expansion and contraction. Previous authors however did not discuss the means by which they did so.

The most likely mechanism for inflation of the test is by cloacal pumping. First, helicoplacoid interambulacral accessory plates have a slight curvature, which do not lend projections or ridges required for muscular attachment and the mechanical advantage required to ratchet the accessory plates outward. Second, helicoplacoids lack epispires. Respiration had to have been carried out either entirely by the tube feet or by a combination of tube feet and another respiratory surface. As other Early Cambrian echinoderms of comparable volume (*Camptostroma*, and *Stromatocystites)* have both tube feet as well as interray epispires, it follows that helicoplacoids required additional surface area dedicated to respiratory purposes. The inferred mode of respiration is through cloacal pumping, a respiratory mode employed by modern holothurians (Farmanfarmaian, 1966; Nichols, 1969; Binyon, 1972). Immediately inside of the cloaca lie the openings to respiratory trees, which extend to upwards of half of the length of the holothurian body. The process by which holothurians respire is described as follows (Hyman, 1955):

The anal sphincter opens and sends a wave of expansion along the cloaca by contracting cloacal suspensors and relaxing cloacal circular musculature, inspiring water. The anal sphincter closes, and a sphincter leading into the respiratory trees opens. Cloacal circular musculature then contracts, channeling water into the respiratory trees.

This mode of respiration has also been argued for in *Amecystis*, an Ordovician cystoid that lacks epispires or other porous respiratory structures (Broadhead and Strimple, 1975), and edrioasteroids included in the group Isorophina, which also lack

epispires (Bell, 1977; Sumrall, 1992). Bell (1977) wrote that the process of pumping water into the respiratory trees in modern holothurians is carried out several times before the deoxygenated water is flushed out. The species *Holothuria surinamensis* carries out 10 to 16 inspirations before flushing the respiratory trees with a single expiration (Crozier, 1916; Binyon, 1972). One particular isorophid, *Spiraclavus nacoensis*, was hypothesized by Sumrall (1992) to inflate the test by means of cloacal pumping. As the volume of the inflated theca was far greater than the collapsed, Sumrall suggested that thecal inflation of *Spiraclavus* required several inspirations. This would have allowed the theca to fill slowly, which would also not disturb the edrioasteroid from its precarious perch, usually on a much smaller brachiopod or bryozoan fragment (Sumrall, 1992). This problem was also likely encountered by and solved in an identical manner by helicoplacoids.

The robust anal pyramid in *Spiraclavus* acted as a valve, keeping the theca inflated by sequestration of water within the respiratory trees (Bell, 1977; Sumrall, 1992). Opening of the anal pyramid and tension of ligaments inferred to have extended for the length of the animal resulted in rapid evacuation of the respiratory trees in *Spiraclavus* and therefore deflation of the theca, likely in response to disturbance.

Helicoplacoids have an accordion-type test while *Spiraclavus* had a telescoping test, so it is more likely that helicoplacoids had ligaments between interambulacral ridges that acted to mechanically contract the test. This premise is supported by interambulacral spines borne by helicoplacoids, the presence of which attests to the grazing of soft tissues by predators that would otherwise occur. More problematic is the lack of a robust anal pyramid in helicoplacoids. It can be presumed that the helicoplacoid anal musculature

was sufficient to close off the theca to the outside environment, as is the analogous soft tissue construction of the holothurian sphincter. Despite being an entirely soft structure lacking any skeletal support, it carries out the same function as the robust skeletal structures found in isorophids.

An additional functional advantage conferred by respiration in this manner is the elevation of the ambulacral portion of the theca in the water column, away from stagnant bottom waters. Furthermore, larger specimens are far more commonly found in the expanded state, suggesting the ability to expand and contract developed later in ontogeny, perhaps as a response to respiratory stress brought on by a decrease in the surface-area-to-volume ratio during growth.

Protective interambulacral spines are not universal in helicoplacoids. Durham (1993) in a taxonomic overview of the group diagnosed five of the nine described species as having interambulacral ridge plates with a spine (Figure 3.17). Well-developed spines are more commonly found in larger individuals, and occur at any point along the interambulacra. In those specimens that bear spines, there are anywhere from 0-9 non-spined plates between spine-bearing plates. Despite an exhaustive search for an interspecific or intraspecific pattern, or a pattern within individuals relative to interambulacral position on the test, none has been found. There does appear to be a greater concentration of spines near the mouth; this is either because of the predatory stress on the water-vascular system, or because interambulacral pleats near the mouth are more mature, and have had a longer growth history, allowing development of spines.

Interambulacral columns make up the bulk of the helicoplacoid test. There are 8-12 parallel pleated ridges that wind continuously in a left-handed spiral from the base of

the lower pole to the upper pole, with ambulacral insertion and loss is usually associated with the mouth. The ambulacra are imbedded within these interambulacra. The interambulacral column immediately below the lower amb terminates at the mouth to accommodate the generation of a one to three new interambulacral ridges between the upper ambulacra (Figure 3.18). New interambulacra are inserted apparently at random at a few other places on the tests of large individuals.

The angle of the interambulacra versus the substrate (normal to the long axis) of the test varies considerably depending on the maturity of the specimen and position on the test. Complete helicoplacoids generally have interambulacra at the lower pole oriented 90º relative to the substrate. Interambulacra continue in this orientation to about 20% of the height of the animal, where the interambulacral ridges make a 70-80 degree left turn, so interambulacra are oriented 10-20º relative to the substrate, which levels to 0º relative to the substrate near the mouth.

In order to better study helicoplacoid construction, Sprinkle and Wilbur (2005) constructed side-layout plating models of the helicoplacoid theca. As the ambulacral areas are central to helicoplacoid symmetry, and as growth radiates from the mouth as in other groups, we created two helicoplacoid models out of modeling clay, coated them in latex, then cut them out along a line opposite the plane of symmetry that cuts through the ambulacral areas. The models we made had 10 interambulacral columns according to the number of interambulacral columns arranged between coils of the ambulacrum, with the loss of one interambulacral column below the mouth and gain of two more between the upper bifurcating ambulacra. The resultant model was an S-shaped curve, with ambulacra central, and 5-6 interambulacral pleats on either side of the ambulacra. The

ridges of the pleats are continuous from the lower pole to the upper, save for the aforementioned gains and losses, with ten interambulacral ridges originating at the base of the curve, and 11 terminating in a spiral at the French-Curve shaped terminus of the model. This model making will be further discussed in the section on helicoplacoid growth.

Mooi and David (1997) argued that growth of the Imperforate extraxial region follows no particular pattern, and that plates are inserted randomly anywhere within the region. Sprinkle and Guensburg (2001) argued contrary to this assertion, that plate insertion originated at the boundary between the imperforate extraxial regions and perforate extraxial region. Perforate Extraxial plates bud off of this zone and grow by increasing plate diameter away from the zone of insertion, while imperforate extraxial elements are inserted, and grow larger through life, resulting in larger plates toward the distal end of the imperforate extraxial region. This pattern is surely the case for some crinoids and eocrinoids, but is not the case in the Early Cambrian taxa *Gogia* or *Camptostroma*. These groups experience plate insertion away from the perforate extraxial region and imperforate extraxial region, at the boundary between the aboral attachment pad and surrounding skeletal tissues. In this sense, helicoplacoid interambulacral areas are homologous to the stem of *Gogia* and pleated skirt of *Camptostroma*. The growth zone can be considered a ring of terminal plates, which bud off interambulacral pleats.

The interambulacral areas in other echinoderms are derived from the perforate extraxial region, and are therefore perforated with orifices for communication the external environment. As previously discussed, the perforate extraxial region is confined

to the upper pole. The two following arguments show that the interambulacral areas are not derived from the perforate extraxial region.

The hydropore, gonopore, and anus are small body openings that allowed for communication of the body cavity with the outside environment (Mooi and David, 1997). Despite an exhaustive search by every helicoplacoid author, these orifices have yet to be found. The most convincing occurrences are not convincing at all; Derstler (1985) claimed to have identified the hydropore in the interior of the mouth frame. Despite stated arguments to the contrary, it appears to be no more than a bubble used in the casting medium. Regardless it is not conclusively a thecal opening.

Durham (1993) figured two suspicious multi-plate breaks in the interambulacral column of a helicoplacoid specimen that he interpreted as the "possible" periproct and gonopore, one adjacent to an ambulacrum and the other four interambulacral columns away (Figure 3.19). Both "openings" occupy the space of a single interambulacral column plate, replacing it with approximately ten small polygonal plates. This interpretation is invalid as the figured specimen is the only known helicoplacoid to show these two openings in the positions that they are found. Other recently collected specimens have similar structures further away from ambulacra. Were the structures recognized by Durham the hydropore and gonopore, they would invariably occur in the same areas in every helicoplacoid specimen studied. These interambulacral gaps are then here reinterpreted as structures regenerated in response to damage, possibly inflicted by a predator. This is evidence that helicoplacoids were capable of skeletal regeneration, as has been documented in extant echinoderm groups (Nichols, 1969).

The perforate extraxial region by definition (Mooi and David, 1997) is also perforated by respiratory structures that vary between groups, but are similar structures called epispires, rhombs, or hydrospires. These are small body openings that allowed for respiratory function. Helicoplacoids respired as do all animals, but did not have the small respiratory openings found in other groups that facilitated gas exchange. Some echinoderms do use tube feet as respiratory structures (Durham, 1993), but it is unlikely that this is the predominant respiratory mode in Early Cambrian groups, which have epispires, excepting helicoplacoids, which were likely cloacal pumpers. This mechanism allows for reduction of the epispire-bearing perforate extraxial region. Further evidence of respiratory trees present in cloacal pumpers is admittedly not likely to surface, as these are internal soft structures with no skeletal support to serve as evidence of their existence, so at this time, the best evidence for this theory is circumstantial.

The two prior arguments indicate that since the interambulacra lack perforations, they could not be derived from the perforate extraxial region. The following inferences ensue from the interpretation that the interambulacral areas are derived from the imperforate extraxial region and not the perforate extraxial region. First, the interambulacral areas of helicoplacoids are not homologous to the interambulacral areas of any other echinoderm group. Second, helicoplacoids are extremely derived for their occurrence so early in the metazoan fossil record. This skeletal design is a drastic modification of the hypothetical ancestral Camptostroma-type echinoderm (see section on derivation of helicoplacoid bauplan). Third, helicoplacoids did not respire in the manner conventional for early echinoderms. In lieu of respiratory openings, helicoplacoids respired in a manner similar to that of the holothurians, which inspire

water through the anus, wherein lie respiratory trees. This solution is also the mechanism for thecal inflation in helicoplacoids. Fourth, the interambulacral areas of helicoplacoids are homologous to the pleated skirt of skeletal tissue surrounding the attachment pad of *Camptostroma* and stalk of *Gogia*.

Imperforate Extraxial: Attachment Pad

The imperforate extraxial region is the imperforate portion of the skeleton dedicated to coelom enclosure and attachment (Mooi and David, 1997). Previous workers have entertained four schools of thought regarding helicoplacoid posture and motility, and therefore the plausibility of an attachment surface. Durham and Caster (1963) and Sprinkle (1976, 1980) entertained the possibility that helicoplacoids may have been unattached and recumbent, with the long axis parallel to the seafloor, positioned with the mouth facing upward. This orientation would have exposed a portion of the ambulacral areas to the sediment surface at all times, which makes this interpretation unlikely. Dominguez-Alonso (1999) argued that helicoplacoids were vagile and infaunal, burrowing by the employment of peristaltic motion of the expandable pleats. Were this the case, evidence in the form of burrows and ubiquitous preservation of complete helicoplacoids perpendicular to bedding would exist; most instead are disarticulated to some degree and parallel to bedding (Durham, 1993; Dornbos and Bottjer, 2000, 2001). The majority of helicoplacoid authors argued that helicoplacoids were not attached, but rather inserted the tapered lower pole into soft substrates, anchoring the animal (Durham and Caster, 1966; Durham 1967, 1993; Bottjer et al., 1999; Dornbos and Bottjer, 2000, 2001; Sprinkle and Wilbur, 2005). These conclusions would indicate that helicoplacoids

lost the imperforate extraxial region and the ability to attach altogether. The same style of substrate interface was argued for the Early Cambrian echinoderms *Camptostroma* (Durham, 1966) and *Lepidocystis* (Durham, 1967c). Both cases have been refuted; *Camptostroma* shows evidence of an aboral suction pad (Guensburg and Sprinkle, 1994; herein) and the lepidocystids attached to skeletal debris, likely in the same manner as *Camptostroma* (Sprinkle, 1973; Sumrall, 1997; and herein), suggesting the attachment surface is homologous to the attachment structures of other echinoderms. Furthermore, the only echinoderm groups that have lost the imperforate extraxial region through geologic time are vagile, such as the holothuroids and echinoids. As helicoplacoids were sessile, it is then likely that they made use of the imperforate extraxial region as an interface with the substrate upon which they lived, a theory supported by but not proven by Derstler (1985).

Mooi et al. (1994) postulated that helicoplacoids were amongst a group of echinoderms that had equal contributions of the axial region, perforate extraxial region, and imperforate extraxial region. Mooi and David (1998) amended this argument through the admission that assignments of skeletal systems to the helicoplacoid test were tenuous at best, while abstaining from assignment of a particular helicoplacoid morphologic feature to the imperforate extraxial region.

The helicoplacoid imperforate is reduced to a disk of skeletal tissue and flesh situated at the tip of the lower pole. Because of the typical biases against echinoderms in general and small skeletal elements in specific, the helicoplacoid lower pole is rarely preserved. Two newly studied specimens retain this lower pole, revealing an area composed of many very small isotropic plates, without any visible suturing (Figure 3.20).

In life, these plates would have been ligatured to one another by soft tissues, which formed a soft flexible pad on the surface of the lower pole. When the edge of the disc was contracted, likely by contraction of the adjacent pleated interambulacral columns, a tight seal would form, which would allow the helicoplacoid to adhere to hard or semi-lithified substrates. A recently studied specimen from the Poleta Formation of the White-Inyo Mountains clearly shows attachment via the lower pole to the posterior border of a *Nevadella* trilobite cephalon (Figure 3.21); a second juvenile specimen shows attachment to a single adult helicoplacoid interambulacral plate upon a bedding surface.

Derstler (1985) also argued that helicoplacoids may have been attached to skeletal debris, a conclusion he arrived at by studying another attached specimen, but gave no indication of the manner in which the helicoplacoid adhered to the skeletal fragment. This mode of attachment via suction to hard or semi-lithified substrates is also found in the Early Cambrian taxa *Camptostroma*, *Schuchertidiscus walcotti*, *Gogia*, and the Middle Cambrian taxa *Totiglobus* (Bell and Sprinkle, 1977) and *Stromatocystites reduncus* (Smith and Jell, 1990). The counterargument that helicoplacoids attached via cementation (Parsley and Prokop, 2004, for example) is invalid. The functional anatomy clearly shows adaptive structures for this type of attachment. Furthermore, most nearly complete specimens are preserved without an intact lower pole. Were the lower pole cemented, disembodied helicoplacoid lower poles would be found attached to skeletal debris. Also, if indeed cemented, the lower pole would be far more resistant to weathering than the remainder of the test, and would therefore be the most likely portion of the helicoplacoid test to be preserved in the fossil record, instead of the most infrequently preserved portion of the test.

As the pad at the lower pole was made of soft tissues surrounding skeletal ossicles, it was an ideal structure for inducing a seal, as the soft tissues would have been capable of conforming to the shape of the substrate. However, this construction shows why the structure is poorly represented in the record, as there are biases in the fossil record against soft tissues and small skeletal elements. The suction attachment also suggests that helicoplacoids were ephemerally attached, and could possibly become unattached by relaxation of the musculature that held it affixed.

Mooi and David (1994, 1997) argued that growth of skeletal elements in this region is unmediated, and that skeletal elements may be added at any position within the Extraxial region. Sprinkle and Guensburg (2001) argued to the contrary; that all skeletal regions have an origin of growth, as in the case of the oculars of the axial region. In stalked echinoderms, the growth of the perforate extraxial region and imperforate extraxial region exists at the boundary between the two regions. New perforate extraxial skeletal plates originated and migrated summit-ward, while new columnals originated and migrated toward the holdfast. While helicoplacoids lack a stalk, the size of the imperforate extraxial skeletal ossicles indicate a similar pattern of growth, but rather than origination of single large ossicles in a zone, imperforate extraxial plates grow from an origin at the center of the disc. These plates must have grown very slowly over the life of the animal, as the diameter of the largest helicoplacoid specimens is not much larger than smaller juveniles.

Bauplan of the helicoplacoids is drastically disparate from all other groups. Schematic representation of the skeletal regions of edrioasteroids, asteroids, and

echinoids (Mooi et al., 1994) compared to a helicoplacoid schematic (Figure 3.22) show how highly modified the helicoplacoid test is. Edrioasteroids represent a basal condition for the Echinodermata, with asteroids and echinoids representing highly derived states.

Growth

Growth in echinoderms, especially in crinoids, has been studied by making side-layout plating diagrams. Traditionally, the theca is cut along a suture in the interambulacral interray, and then laid out flat, keeping the plates that share a suture contiguous, not unlike making a Mercator-Projected map out of a globe (Ubaghs, 1978). The result is a two-dimensional surface representing the three-dimensional echinoderm theca. Sprinkle and Wilbur (2005) made highly modified versions of these plating diagrams for helicoplacoids, in order to better understand growth. Since helicoplacoid bauplan is drastically different than that of crinoids, with triradial symmetry and a lateral mouth, and since plate growth radiates in two directions away from the mouth, with relatively unbroken interambulacral columns paralleling the ambulacral areas uniformly throughout the length of the theca, we created diagrams with the down-going ambulacrum as the key to symmetry. We created helicoplacoid models out of modeling clay according to test proportions encountered in the fossil record, and then covered these in latex. Anatomical features, including interambulacral areas and ambulacral areas were then drawn on the surface. The latex cover was removed from the clay by cutting directly opposite the lower ambulacrum, resulting in a curved strip, ambulacra central, with 4-6 IA columns on either side.

Two models were made to accentuate the difference in overall theca shape between juveniles and adults. The first model was light bulb ("inverted-pear") shaped, with a circular base, inverted conical lower theca, and a hemispherical top. This overall shape is more common in adult helicoplacoids. The mouth was placed at 58 percent of the thecal height from the base; we used an 18-degree plating spiral angle relative to horizontal, and the lower ambulacrum turned vertically down toward the base at about 25 percent of thecal height and ended just below. These shape and plate-spiraling specifications are similar to those of several helicoplacoids figured and described by Durham (1967, 1993) as *Helicoplacus everndeni, H. gilberti*, *Westgardella firbyi*, and *W. blancoensis* (Sprinkle and Wilbur, 2005).

The second model was more spindle-shaped and thinner, with a long, inverted conical base and summit, and a rounded central portion connecting the two together, approximating the spindle shape common in juvenile helicoplacoids. The mouth was placed at 60 percent of the thecal height from the base, but we used a higher 35-degree spiral angle to the horizontal, and both the lower and upper ambulacra turned vertically toward their respective poles at about 25 and 75 percent of thecal height and extended somewhat further. These shape and plate-spiraling specifications are similar to those found in the helicoplacoid described by Durham (1967, 1993) as *Waucobella nelsoni*, the Paul and Smith (1984) specimen of *Helicoplacus gilberti*, and some small specimens of *Helicoplacus and "Westgardella"* from our new collections (Sprinkle and Wilbur, 2005).

The result was an S-shaped curve, resembling a "French Curve" drawing implement or the sound hole in a violin (Figure 3.23, 3.24). The length to width ratio of the adult model was 6.7:1, while the juvenile was 4.2:1 (Sprinkle and Wilbur, 2005). The

width of the strip was not greatly increased upper- poleward of the mouth as the addition of two new interambulacra between upward spiraling ambulacra is accommodated for by the loss of an interambulacrum immediately below the mouth. The lower pole is curved relative to the remainder of the strip as the interambulacral pleats that make up the test make nearly a 90º turn in order to form a tapered tip. The lower pole ends in a broad lunate curve, accommodating the surface of the lower pole. Each lower pole interambulacral pleat extends to the boundary between the theca and attachment pad.

The upper pole terminates in a broad sigmoidal curve, as interambulacral columns terminate before reaching the small patch of irregular plating that represents the terminus. Not all interambulacral columns reach the terminus; some merge with adjacent interambulacral pleats just below the summit. Overall, the upper pole represents a geometric spiral, and may represent a Fibonacci Sequence (Gould and Katz, 1975; Sprinkle and Wilbur, 2005). The uppermost ambulacral column is recognized by Durham (1967, 1993), Paul and Smith (1984) and Derstler (1985) to terminate well below the summit of the upper pole, but these observations were made on adult specimens only. Spindle-shaped juvenile helicoplacoids have a much more tapered upper pole, in which the upper pole more closely resembles the long slender lower pole. Ambulacral areas in these juveniles extend to the uppermost reaches of the upper pole, and terminate coincidently with the adjacent interambulacral columns. In adults however the failure of the uppermost amb to reach the terminus is universal.

The plating strips derived from this model making elucidates the mode of growth in both juvenile and adult helicoplacoids. Ambulacra and interambulacra are necessarily integrated in function, as expansion of the interambulacral pleats requires cooperation of

the adjacent ambulacra to which they were attached. This suggests that interambulacra and ambulacra were also coordinated in growth, a finding supported by the S-shaped plating strips. If one region grew faster than the other, shear between these regions would rupture the soft tissues holding these skeletal regions together.

Helicoplacoids grew through two modes; insertion of skeletal ossicles and expansion of already existing plates. New ambulacral floor and cover plates were inserted biserially by ambulacral terminal plates, and interambulacral ridge and interambulacral terminal plates inserted accessory plates similarly. Insertion of ambulacral and interambulacral plates was coordinated, as ambulacra were locked into place relative to adjacent interambulacra.

Plating of all types is smaller toward the pole and larger toward the mouth, which indicates the oldest plates are near the mouth, and youngest plates are away from the mouth toward both poles. This in turn implies that plate insertion originated at both poles and that helicoplacoids grew larger by serial plate insertion away from the mouth. Juveniles then had the three ambulacra, a lateral mouth, and upper and lower pole found in adults. They differ only in plate size, overall thecal shape, and relative ambulacral length.

Modern echinoids grow in a similar manner, with plate insertion at the summit of the organism, inflating the test away from the mouth, which is where the oldest plates are found. Unlike modern echinoids, however, helicoplacoids had two such growth zones. A ring of plates responsible for plate insertion existed in a very narrow ring near the summit and in a broader ring at the base of the lower pole. The upper ring served to sequester the axial skeleton from the perforate extraxial skeleton; the ring at the lower

pole served to sequester the axial skeleton from the imperforate axial skeleton. The upper and lower ring had 10-12 ocular plates responsible for secreting the continuous interambulacral pleats from the lower to the upper pole (Figure 3.25).

Helicoplacoid plates also grew in length and width after their insertion. Newly inserted interambulacral and ambulacral plates (including all plates in juveniles, which have an entire theca composed of immature "newly inserted plates") have blunted edges, a high width to length ratio, and usually have a series of incised grooves along the distal edge parallel to the axis of the interambulacral pleats. Older, more mature plates (interambulacral and ambulacral plates in the vicinity of the mouth and plates in large specimens) are larger in both dimensions, but grow disproportionately in length, resulting in plates with a much lower width to length ratio. Frequently, these larger plates develop spines at the tips, which in conjunction with increase in length serves to distort the parallel ridges so prevalent in juveniles. These grooves exist along the edges of nearly all helicoplacoid plates from blunt to spined plates, which can be arranged to show a growth series of individual plate elements (Figure 3.26, 3.27).

The increase in plate length also makes the plates appear to be thinner. Juvenile plates are no thicker than adult plates; it is the change in the other dimensions of the plate that make it appear as if this is the case. In summary, plates grow disproportionately, with more marked increase in length than width, and do not increase in thickness.

Helicoplacoid interambulacral columns are capable of three distinct postures. The first is in a contracted state, with adjacent interambulacral pleats drawn together so that the lateral faces of each ridge plate abut (Figure 3.28). The second common posture is fully expanded, with ridges of the interambulacral pleats at a maximal distance away

from each other, and accessory plates flanged out to toward either pole (Figure 3.29). The third posture is partially expanded/contracted, with some space between ambulacral pleats, and interambulacral pleats distended slightly (Figure 3.30). Usually specimens in this state show ridge plates oriented either upward or downward, and less commonly, pointed directly outward. A variation of this posture is found in only a handful of well-preserved specimens. These show interambulacral pleats completely distended and pointed toward the lower pole, exposing the superior lateral faces of each interambulacral pleat. The distal-most portion of each pleat overlaps the proximal-most portion of each pleat below it, protecting the soft tissues at the base of the interambulacrum. The end result is a shingle-like pavement on the surface of the theca (Figure 3.31).

The likely selective advantage of this plate orientation is for protection of soft tissues in the interambulacral pleats, and of the ambulacral areas. Ambulacra were capable of closing the cover plates in order to protect the soft tissues associated with the water vascular system, but in specimens with plates facing outward, no ambulacral areas are visible, despite being complete and large enough to show evidence of at least a single ambulacrum. This suggests that ambulacra had great potential as a food source, as they had as many as three lines of defense; spines, cover plates, and interambulacral pavement.

Depending on the posture of the helicoplacoid, the theca can appear drastically different. Fully contracted interambulacral areas show only the distal edges of plates, which are rounded in juveniles and sharper edged in adults, and have incised parallel grooves. Slightly distended, the plates point the edges downward, exposing the superior or inferior faces of the interambulacral pleats, making overall plate morphology appear

flat and wide, obscuring the ridge plate grooves. Fully extended, ridge plates appear much as they do completely retracted, but much longer. These evident differences in helicoplacoid posture and the change in plate morphology through ontogeny were originally misinterpreted as taxonomic signals by Durham (1993), which resulted in a misrepresentation of the overall diversity of the group, a shortcoming that will be discussed in the forthcoming section on helicoplacoid systematics.

Ontogenetic timing of the oculars during development of the animal can solve the problem of terminating interambulacral columns and ambulacral tips away from the growth zones at the lower and upper poles. As previously discussed, ambulacral areas of juvenile helicoplacoids have been found to extend to the tip of the upper pole, while adult ambulacra terminate well away from either pole. Furthermore, an interambulacral column terminates just below the mouth, and 1-3 new interambulacra are generated poleward of the mouth between the upward-extending ambulacral areas. In juveniles, plate-generation occurs entirely at the poles, with oculars responsible for generation of ambulacra adjacent to oculars responsible for generation of interambulacral pleats. As the animals get larger, the oculars responsible for the ambulacra are "shut off," which seals the ambulacrum between two adjacent interambulacral pleats. Ambulacra and interambulacra continue to grow through life by plate elongation, but no new ambulacral plates are added. This requires coordination of ambulacral and interambulacral growth, so that there is no shear between adjacent plates. The same method of temporal ocular termination can be applied for interambulacral pleats that appear to terminate or originate along the test; a termination is the developmental "turning off" of an ocular, and the

origination of a new interambulacral pleat is the "turning on" of a new ocular away from the mouth.

Paleoecology

Helicoplacoids were first considered to have a lower pole inserted in soft substrates (Durham, 1967, 1993), a concept that was later modified to "sediment sticking"(Bottjer et al., 1999; Dornbos and Bottjer, 2000, 2001) to incorporate the importance of the substrate surface, with the same mode of insertion. There are two reasons for these conclusions. First, the lower pole, which has the morphological machinery for suction attachment, is very rarely preserved, for reasons discussed herein. It was therefore understandable that previous workers overlooked the morphology interpreted herein. Second, some helicoplacoids are preserved with most of the test splayed out upon a bedding surface, with the lower pole perpendicular to the bedding surface. X-radiographs confirm that these animals were preserved in graded beds, suggesting obrution deposits knocked over and preserved these animals in-situ (Dornbos and Bottjer, 2000, 2001). The morphological evidence, and specimens attached to trilobites and other helicoplacoid plates overwhelmingly support the theory that helicoplacoids attached to debris or semi-lithified substrates. The "imbedded" lower pole mentioned by Dornbos and Bottjer (2000, 2001), which is also seen in specimens collected by the author, are probably cases in which the lower pole of adult specimens silted over through the lifetime of the organism, before an obrution deposit smashed the animals against the bedding surface and buried them.

It was also mentioned in Bottjer et al. (1999) and Dornbos and Bottjer (2000, 2001) that helicoplacoids were imbedded into microbially bound substrates that maintained a sharp boundary at the sediment-water interface. The advent of widespread burrowing organisms in the later Early Cambrian destroyed the matgrounds upon which helicoplacoids were inserted, creating a soupy layer at the sediment-water interface, which in turn caused the helicoplacoids to go extinct (Bottjer et al., 1999; Dornbos and Bottjer, 2000, 2001). While trilobites may have been the optimal substrate, a microbially bound matground could also serve as a suitable substrate for adhesion by suction, rather than a bound substrate for insertion. These would not have provided the same degree of support as a flat skeletal fragment, but would have been sufficient in very low energy environments.

As these organisms were not cemented, and were not permanently attached, it is possible that helicoplacoids may have been able to search out an optimal substrate, similar to the motility that modern comatulid crinoids are capable of. This theory is supported by a newly discovered juvenile helicoplacoid attached to a disarticulated adult helicoplacoid plate (Figure 3.32). As the animal grew in size, the single plate would eventually be rendered insufficient to anchor an animal the size of an adult helicoplacoid, requiring the search for and use of a more suitable substrate.

The theory of suction attachment, while contrary to the type of interface hypothesized by Durham (1967, 1993), Bottjer et al. (1999), and Dornbos and Bottjer (2000, 2001) bolsters the claim that the decimation of matgrounds resulted in the demise of the helicoplacoids (Bottjer et al., 1999; Dornbos and Bottjer, 2000, 2001). Very few helicoplacoids have been found attached to skeletal fragments, which would mean that

the vast majority of the animals were attached to mats, which, if altogether destroyed, would drastically crop the overall population. The suction attachment pad itself was an evolutionary innovation that proved successful only during the Cambrian, with the Early Cambrian groups *Gogia*, *Camptostroma*, the helicoplacoids, *Schuchertidiscus*, the lepidocystids, and later Middle Cambrian eocrinoids and edrioasteroids employing it as a means of attachment. Beginning with the Late Cambrian and continuing into the second radiation of echinoderms in the Early Ordovician, suction pads were altogether lost, as sessile echinoderms developed cemented holdfasts to affix directly to hardgrounds novel to the Post-Cambrian world and more widespread carbonate reefs and bioherms (Guensburg and Sprinkle, 2004).

As previously discussed, it was mentioned by Durham (1963), Sprinkle (1976, 1980), and Dominguez-Alonso (1999) that helicoplacoids were not attached, but rather free living. This would result in befouling of the ambulacral areas, which along with the evidence for a lower-pole holdfast structure make this theory altogether very unlikely.

Helicoplacoids are most commonly preserved as external molds, without retaining any skeletal remains. Oddly enough, many helicoplacoids have a steinkern. These are vital for the understanding of test interiors, as they show the folding patterns of the interambulacral areas, and flooring plate anatomy. The presence of steinkerns is rarely addressed in helicoplacoid literature; the best discussion of echinodermal steinkerns exists in Sprinkle, 1973. Therein, any material existing between the internal walls of echinoderms is presumed to be post-mortem infilling of the theca via tears in the body wall. However, the very best preserved complete helicoplacoids, including those with no evidence of test disarticulation, show steinkerns. The sediment within the theca of

helicoplacoids is probably ancient gut contents, which conform to the shape of the flattened post-mortem test of helicoplacoids after decay of gut tissues.

Helicoplacoids were passive filter feeders, ingesting any material that came into contact with the ambulacral areas, which would have included a soft rain of organic debris and fine-grained siliciclastic material, all of which was indiscriminately ingested. Digestion of the organic material within the ingested mélange would require a gut rather than a single orifice as in some asteroids. This then is also suggestive that helicoplacoids indeed have a mouth opening and anus, rather than a single opening. Again, the location of the anus is enigmatic, but probably was located at the upper pole, where the remnant of the perforate extraxial region is sequestered.

Systematics (Historical)

Helicoplacoid systematics was first discussed in detail in the original paper on the group, wherein Class Helicoplacoidea was erected to house the two new species of echinoderms discovered. The class diagnosis is as follows (Durham and Caster, 1963):

> Free living, fusiform placoid echinoderms with spirally pleated, expansible test; apical and oral poles at opposite extremities; columns of plates arranged in a spiral; ambulacra and 'interambulacra' present; new 'interambulacral' plates originating at the apical pole and becoming more oral in position as subsequent plates are added (origin of ambulacral plates obscure). Lower Cambrian, California.

The authors had available to them a paucity of specimens collected by field camp students, from which they discerned two morphotypes. The first, named *Helicoplacus gilberti* Durham and Caster, 1963 was described as having a test composed of four complete whorls of interambulacral pleats, rounded distal interambulacral plate edges

with "fine longitudinal ridges" (called "incised parallel grooves" herein), spines on every fourth to ninth interambulacral plate, and an overall thecal height of 35 mm. The second, *Helicoplacus curtisi* Durham and Caster, 1963, was diagnosed as having angled rather than rounded distal edges to the interambulacral ridge plates, interambulacral ridge plate edges lacking the longitudinal ridges, long spines on the medial portion of the test, and occurring with thecal heights of up to 75 mm (Durham and Caster, 1963). In his 1964 paper, Durham wrote that there are at least five, but more likely six species of helicoplacoid, but because of the medium (a magazine article rather than a scholarly journal) he neglected to describe them.

The treatise chapter written by Durham and Caster (1966) included the introduction of Family Helicoplacidae, the diagnosis for which was as for the class (Durham and Caster, 1963). Diagnosis of the genus *Helicoplacus* included the presence of 10 interambulacral columns between coils of the single, branched ambulacrum. As is the case with treatise chapters, no new taxonomic insight into specific diversity was discussed.

Revisions to the group were made in Durham 1967, wherein two new genera were added to the class, warranting a description of the genus *Helicoplacus*, which was substituted for by a description of the class in the original space-delimited *Science* article erecting the group. Genus *Helicoplacus* was diagnosed as having large interambulacral ridge plates, simple ambulacral plating, and a branched ambulacrum. The type species for the genus was designated *Helicoplacus gilberti*, a selection that was overlooked in the original paper on the group.

The description of *Helicoplacus gilberti* was expanded to include the following: interambulacral plates have 3 to 4 longitudinal ridges and poorly developed spines away from the mouth, and interambulacral plate lengths of 2 to 3 times width. It must be noted here that Durham considered the mouth to be at the summit, so "poorly developed spines away from the mouth" means away from the summit, not the mouth as it is now understood. This point follows for all systematic descriptions carried out by Durham, which encompasses all descriptions prior to the new descriptions included in this work. *Helicoplacus gilberti* was elaborated by inclusion of the following characters: interambulacral plates are heavy, distally angulate, and lacking in longitudinal ridges; some plates developed long slender spines (Durham, 1967).

The genus was also augmented by the addition of two new species. The first, *Helicoplacus everndeni* Durham, 1967, was diagnosed as follows: angulate distal edge to interambulacral plates, length of interambulacral plates 2 to 3 times width, 2 longitudinal ridges at the edge, and fewer toward the interior of the pleat, and broad, low spines on every second to fifth plate. The second, *Helicoplacus firbyi* Durham 1967, was diagnosed as follows: more than 10 interambulacral areas between the ambulacrum, short ridge plates with length less than twice the width, thin distal edge, with two longitudinal ridges, and no spines (Durham, 1967).

Genus *Waucobella* was erected to include a unique and problematic helicoplacoid. The genus was diagnosed as follows: fusiform test, long, numerous narrow interambulacral plates that almost universally bear spines, complex ambulacra, 2 interambulacral pleats between the upper ambulacral branches, and twelve interambulacral pleats between the spiraling ambulacrum. The new species for which the

genus was erected, *Waucobella nelsoni* Durham, 1967, was diagnosed as follows: 60 mm long test, complex ambulacrum consisting of five small medial plates and three to four lateral plates with pores between adjacent plates for the passage of tube-feet, and spines occurring on at least every other interambulacral plate, each of which was slightly larger than a non-spine bearing plate (Durham, 1967). It requires mention here that Durham's ambulacral description describes an amb as Durham understood it to be, with a large medial ridge, and tube-feet emerging from the basal pores (Figure 3.9), a view that is incorrect.

The prior five helicoplacoid species were all incorporated in Subclass Helicoplacida based on the fusiform to pyriform test comprised of expansible pleats, for the most part to distinguish these from the monotypic Subclass Polyplacida, erected to house the new species *Polyplacus kilmeri* Durham 1967, another problematic helicoplacoid, represented by one complete and one partial specimen on a single slab of rock. The Subclass diagnosis is as follows: test built of pleats comprised of a mosaic of small plates, which were presumed to be interambulacral, with ambulacra unknown. The genus was diagnosed as having numerous expansible pleats, numerous conical projections upon the distal tips of the interambulacral columns. The species was diagnosed as having a 50 mm high test, and conical projections along the interambulacral ridge every 2.5 to 4 mm, a 2.5 mm interambulacral ridge height above the adjacent grooves, and conical projections that rise 1 mm above the remainder of the interambulacral column (Durham, 1967). The most diagnostic of all characters for this echinoderm is the myriad small plates that make up each interambulacral ridge. While

there is no ambulacrum identified by Durham, the interambulacral ridges appear to be made of ambulacral cover plate sheets.

The final systematic work on helicoplacoids (Durham, 1993) amended previous familial, generic and specific descriptions, added several new characters, reassigned two species to a new genus, and erected two new species. The work was based on new specimens, and sixteen years worth of new observations on anatomy. The impetus for the new study seemed to be a new interpretation of ambulacral morphology and interambulacral ridge plate characters.

Family Helicoplacidae was rediagnosed to include the findings on the restudied ambulacral areas. The diagnosis is as follows: pores for the passage of tube-feet are found not at the lateral junction of adjacent flooring plates but in the superior/inferior margin of stacked covering plates (Figure 3.9), interambulacral ridges are adorned with either ridges or pustules, and eight interambulacral columns lie between the coiled ambulacrum. Genus *Helicoplacus* was amended to include only those helicoplacoids with the aforementioned plate ornament. The genera previously described required redescription to take into account new observations on the group and new divisive characters.

Helicoplacus gilberti Durham and Caster 1963, the first helicoplacoid species to be named, was rediagnosed with the following characters: rounded profile to interambulacral ridge plates, with "about" 5 ridges, and interambulacral plate lengths of three to five times plate widths (Durham, 1993). *Helicoplacus everndeni* Durham 1967 was rediagnosed with the following characters: interambulacral ridge plates compressed,

with two ridges on distal edge, no spines but occasional plates with "distal edge obtuse," and interambulacral plate length of two to three times plate width (Durham, 1993).

Two new species of *Helicoplacus* were added to the genus. The first, *Helicoplacus casteri* Durham 1993 was diagnosed as follows: interambulacral ridge plates compressed with two or three ridges, plate length of three to four times width, and no spines, but again some plates show a slight angulation (Durham, 1993). *Helicoplacus guthi* Durham 1993 was diagnosed as follows: interambulacral ridge plates have pustulose ornament, rounded profile, and interambulacral ridge plate length of four to five times width (Durham, 1993).

The new family Westgardellidae was erected to include helicoplacoids with, among other characters, a newly studied ambulacral morphology that differentiated the group from the Helicoplacidae. The family diagnosis is as follows: pores for the passage of tube feet in the margins of laterally adjacent ambulacral covering plates (Figure 3.9), 10 or 12 interambulacra between the spiraling ambulacrum, and interambulacral ridge plates lacking ornamentation. The diagnosis of the new genus *Westgardella* is as follows: 10 ambulacral columns between the spiraling ambulacrum, smooth interambulacral ridge plates, plates bearing angulations or prominent spines, and tube foot pores between laterally adjacent ambulacral covering plates (Durham, 1993).

Genus *Westgardella* included three species; two removed from genus *Helicoplacus* and deposited into the new group, and one newly named. *Helicoplacus curtisi* Durham and Caster 1963 was renamed *Westgardella curtisi* Durham and Caster 1963, and rediagnosed as follows: angulate distal edges to interambulacral ridge plates,

interambulacral ridge plate length one to 1.5 times width, periodic plates bear spines, and an overall more fusiform test than that of *H. gilberti* (Durham, 1993).

Helicoplacus firbyi Durham 1967 was renamed *Westgardella firbyi* Durham 1967, and rediagnosed as follows: interambulacral columns composed of many small plates, with length one to two times width, and no apparent external plate ornamentation (Durham, 1993).

The new species *Westgardella blancoensis* Durham 1993 was diagnosed as follows: unornamented interambulacral ridge plates, with length approximately equal to width, and occasional angulation to distal edge of ridge plates. The holotype of this new species was originally diagnosed as a paratype of *Helicoplacus gilberti*, a change that reflects the lack of late ornamentation diagnostic of the genus (Durham, 1993).

Genus *Waucobella* was included in Family Westgardellidae because of a similar tube-foot pore orientation upon the supposed cover plates. It differs from genus *Westgardella* by having 12 interambulacral pleats between the coiled ambulacrum. The specific description of *Waucobella nelsoni* Durham 1967 was altered to a diagnosis as for genus; namely a helicoplacoid with ambulacral pores between laterally adjacent cover plates (Figure 3.9), and 12 interambulacral columns between the coiled ambulacrum (Durham, 1993). The description that served as a diagnosis from Durham's 1967 is more complete, including the expansive tessellate ambulacral areas as a diagnostic characteristic (Durham, 1967), a nontrivial trait that will be returned to.

Polyplacus kilmeri Durham 1967 was not reevaluated; the diagnosis for the genus and species was based on the interambulacral ridge composition of numerous small plates arranged in expansible pleats. Durham posited that *Polyplacus* interambulacra are

suggestive of the ambulacra of genus *Waucobella*, a nontrivial point subscribed to herein (Durham, 1993).

Amended Systematic Descriptions

Whereas the systematic paleontologist delights in the "eureka" moments of discovery of taxa heretofore unknown, and describing these new organisms with new names devised to honor the group, collectors, and past heroes of the field, it is my duty herein rather to synonymize several of the species in Class Helicoplacoidea. The previous taxonomic work carried out in Durham and Caster 1963 and 1966, and Durham 1967 and 1993 overestimated the total number of species, primarily because of misinterpretations of ontogenetic stage and of plate posture. I hereby propose that there were not the nine original species described, but rather two, as the remaining seven are solely variants on the original themes found within two distinct groups.

Durham's misevaluation of the taxonomic diversity has two root causes; ontogeny and posture. Once the original misinterpretations were established, further misidentification followed based on misinterpretations of ambulacral morphology.

Ontogeny of the interambulacral ridge plates is the first and most important obscuring detail. Young helicoplacoid plates have rounded edges and a series of grooves parallel to the long axis of the plate. Over ontogenetic time, disproportionate growth makes plates apparently longer and changes the plate profile to a sharp edge. In these "mature" plates, grooves are still apparent. Some plates grow spines; a growth series can be constructed for spine bearing plates as well, with intermediate "angulate" plates, still bearing grooves along the edge.

Plate ontogeny coupled with the posture of helicoplacoid interambulacral pleats has served to further obscure the systematics of this group. Helicoplacoids in the fully contracted state interpose the superior face of the interambulacral column with the inferior face of the column adjacent to it, exposing only the distal edge of the interambulacral column. Interambulacral ridge plates are perpendicular to the long axis of the animal, and the interambulacral accessory plates are folded immediately behind of and parallel to the ridge plates. Fully expanded helicoplacoids maintain the same perpendicular orientation to the interambulacral ridge plates, but the accessory plates ratchet outward so that they are perpendicular to the ridge plates, causing the accordion-like expansion of the test. This posture exposes the superior and inferior faces of the interambulacral ridge plates, making them appear longer than they would otherwise.

The most common helicoplacoid posture is partially contracted. In this orientation, the interambulacral ridge plates than are distended and oriented most commonly toward the lower pole. Each trio of plates forming the interambulacral pleat, one ridge plate and a lower and upper accessory plate, acts in concert to distend the upper edge of the ridge plate, and retract the lower edge of the ridge plate. This is accomplished by relaxation of the mutable collagenous tissues holding the distal edges of the accessory plates together, and rotation of the lower accessory plate (Figure 3.16A-C). This exposes the superior faces of the interambulacral ridge plates, making them appear as if they are long and unornamented. The ornament that invariably exists is along the downward-pointing plate edge, which is readily observable if the specimen in question is oriented along the long axis, along the trend of the interambulacral plates. Ultimately, these three different postures can make it appear as if there are three different plating

types, which, when coupled with plate ontogeny, can account for the apparent diversity described in Durham and Caster 1963, Durham 1967, and 1993.

Within genus *Helicoplacus*, there are four named species, each diagnosed generically as having plate ornament. Of these, three species have ridges along the distal edges of the interambulacral ridge plates. Therefore, the only distinguishing characteristics between the three are as follows: *Helicoplacus gilberti* has a rounded plate profile, five distal ridges, and a plate length to width ratio of 3:1 to 5:1; *Helicoplacus everndeni* has a flattened plate profile, angulation at the edges of some interambulacral ridge plates, two distal ridges, and a plate length to width ratio of 2:1 to 3:1; *Helicoplacus casteri* has a flattened plate profile, angulation at the edges of some interambulacral ridge plates, two to three distal ridges (Durham, 1993).

The most obvious problem with these diagnoses is the overlap in plate length to width ratio. A helicoplacoid with a length to width ratio of 3:1 could be diagnosed as any one of the three species. It can be presumed that the discussion of length to width ratios was an attempt to quantify an "eyeballed" difference that was more qualitative in nature. Furthermore, the rounded plate profile in *H. gilberti* differs from the flattened plate profiles of *H. everndeni* and *H. casteri* only as an ontogenetic series. As previously discussed, helicoplacoid plates grow disproportionately in length after insertion, making plates appear flatter as they grow. Furthermore, the plates in the type specimen of *H. gilberti* are completely retracted, while the interambulacral pleats in the type specimen of *H. everndeni* are partially retracted, with the ridge plates distended and pointed downward. Along with the angulations that develop later in ontogeny, these two sets of specimens at different ontogenetic stages and with differing postures were misinterpreted

as two different species. *H. casteri* again differs from *H. gilberti* only in the lack of distal angulations and fewer distal grooves in the latter; again this can be explained through ontogeny. Therefore, the helicoplacoids described as *H. gilberti*, *H. everndeni*, and *H. casteri* represent the same species. *Helicoplacus gilberti* Durham and Caster 1963 and *Helicoplacus curtisi* Durham and Caster 1963 are both potential senior synonyms, but as Durham (1967) designated *H. curtisi* as the type species for the genus, it is given priority. Therefore, all aforementioned specimens are referable to the taxon *Helicoplacus gilberti* Durham and Caster 1963.

Helicoplacus sp. b is the designation given the incomplete specimen from British Columbia, Canada. The helicoplacoid is partial, and therefore is not namable, but Durham thought it to represent a new species (Durham, 1993). It has a rounded plate profile, angulations on the distal edges of a few of the interambulacral pleats, well defined grooves on the surfaces of the interambulacral ridge plates, and length to width ratios of 1.5 to 1 (Figure 3.33). This represents yet another occurrence of *Helicoplacus gilberti*; the plates are seemingly narrower as this specimen is represented by solely the lower pole, which was a place of plate insertion during the life of the organism, and so would have the most immature plates on the lower theca.

Further taxonomic overrepresentation is a product of chemical precipitates and chemical weathering. Helicoplacoid molds in shale are prone to accumulations of oxides on the surfaces of the mold. When cast, the fractal oxide patterns leave series of convoluted ridges and valleys upon the surfaces of the interambulacral ridge plates. Derstler (1985) commented on this phenomenon in specimens within the UCMP and UC Davis collections from the White-Inyos, and noticed that it made a specimen appear

superficially like *Polyplacus*. The same oxides are found in many Indian Springs specimens, at times so heavy it renders the specimens unusable for morphologic study. Furthermore, weathering of the molds can pit the surface of the fossils, creating apparent small bumps upon plate surfaces of specimens cast in latex. This weathering is responsible for the "pustulose" plate ornament adorning the surfaces of the plates of "Helicoplacus guthi" (Durham, 1993) (Figure 3.34). This is proven by the appearance of the same pustulose ornament on the internal surfaces of the skeletal plates upon the counterpart, indicating that the pustules were a case of weathering and not ornament, which exists only upon external surfaces. This species name is no longer valid; the type specimen is synonymous with *Helicoplacus gilberti*. An additional specimen figured in Durham, 1993 (fig. 8-2) is a second example of the effects of taphonomic alteration of skeletal material. Named *Helicoplacus* sp. A, this is another example of an altered specimen of *Helicoplacus gilberti*.

Family Westgardellidae was distinguished from Family Helicoplacidae by two characters. The first of these is ambulacral. Tube foot pores in the Helicoplacidae were located at the junction of two vertically ("contemporary" in Durham, 1993) arranged cover plates, while in the Westgardellidae, tube foot pores were located at the junction between horizontally arranged cover plates (Durham, 1993) (Figure 3.9). As previously discussed, the "tube-foot" pores in the Helicoplacidae were misdiagnosed ligament pits. The "cover plates" of the Westgardellidae were misdiagnosed distended floor plates. In this regard, the ambulacral areas of Family Helicoplacidae and Family Westgardellidae are indistinguishable.

The second characteristic is interambulacral. The Helicoplacidae had eight interambulacra between the spiraling ambulacra. Westgardellidae had 10 to 12 interambulacra between the spiraling ambulacrum. Arrival at these numbers is arbitrary; Durham used solely the type specimens to arrive at these numbers. While certainly not arbitrary, helicoplacoids show great variation in interambulacral structure. Many specimens have interambulacral columns that split or are generated away from the mouth. The only interambulacral columns that are universally added/reduced are the IA inserted immediately below the mouth, and the one to three interambulacra added between the C and D ambulacrum. Such being the case, the portion of the test that is preserved greatly influences the taxonomic interpretation. The specimen for which the diagnosis of eight interambulacra between the ambulacra was made, the holotype specimen of the type species of genus *Helicoplacus*, UCMP 37847, is preserved with the mouth at the far right edge of the specimen. Were the animal rolled to the side during preservation so that the mouth was central, the generated amb immediately below and to the right of the mouth would show, which would have changed the diagnosis to nine interambulacra between the ambulacrum. Furthermore, the holotype of *Helicoplacus everndeni* (UCMP 14770, figure 2-1 in Durham, 1993) shows between six and seven interambulacra between ambulacra, not the diagnostic eight.

Furthermore, because of the generation of one interambulacral area below the mouth, two interambulacral areas between the upward-spiraling ambulacra, and the termination of the lower of these, the vertical trend taken on a single specimen will vary greatly. On an ideal helicoplacoid with eight interambulacral areas between the amb, generation of one down going interambulacral ridge below the mouth, and generation of

two up going interambulacral columns, and no other losses or generations, there are anywhere from eight to eleven possible interambulacral areas between ambulacra. The vertical transect from the lower amb on the lowest portion of the test to the amb just to the right of the mouth will show nine interambulacra. The vertical transect from the lower ambulacrum on the lowest portion of the test to the ambulacrum just to the left of the mouth will show eight interambulacra. Finally, the vertical transect from the lower ambulacrum on the lowest portion of the test to the D ambulacrum amb just to the left of the termination of the C ambulacrum will show ten interambulacra (Figure 3.35).

Undoubtedly Durham was presented with an array of specimens that showed quite a bit of intraspecific variation because of the unstandardized interambulacral terminations/generations, but because of the paucity of nearly complete specimens, those that were nearly complete preserved as the torchbearer for a new taxon despite these inconsistencies. Therefore, there is no basis for the delineation of "Family Helicoplacidae" and "Family Westgardellidae." As Family Helicoplacidae is the senior synonym, having been established in Durham and Caster 1966, all helicoplacoids from these two former groups are referable to the Helicoplacidae.

Genus *Westgardella* is diagnosed by the presence of ten interambulacral areas between the spiraling ambulacrum, smooth plate surfaces, distal angulations or spines, and tube foot pores between laterally adjacent cover plates (Durham, 1993). As previously discussed, the tube foot pore diagnosis and presence of ten interambulacra are invalid. Furthermore, the smooth plate surfaces described by Durham are a case of misinterpreted plate posture. Fully retracted plates expose only the distal edges of the interambulacral plates, while a partially retracted specimen can have plates oriented

downward or upward. The "smooth plate surfaces" (Durham, 1993) are the superior faces of the interambulacral ridge plates, which in many cases have rounded and grooved edges if viewed on edge. Frequently a single specimen will show differing plate postures at different positions on the test, and appear as if they are chimeras, composed of "*Helicoplacus*" type and "*Westgardella*" type plating.

The presence of spines is also invalid as a diagnostic signal, as smaller juvenile helicoplacoids have no spines, and larger specimens have spines. Based on this initial observation, it was perceived that a growth series of spine development could be assembled. Juvenile or "*Helicoplacus gilberti*" (as diagnosed by Durham, 1993) type plates through ontogeny develop angulations, turning into "*Helicoplacus everndeni*" type plates. Further development results in long thin spines, like those found in "*Westgardella curtisi*." Some specimens (i.e. UCMP 37849) show well-developed spines at the upper pole, which poses a problem, as the upper pole represents the origin of plate insertion, and should therefore have the least mature plates. The presence of mature, spine bearing plates can be explained through a decrease in growth rate. Helicoplacoids must have slowed the rate of plate insertion later in ontogeny. When the rate of insertion slowed to zero, the recently inserted plates continued to develop, resulting in the presence of spines near the center of plate insertion. Therefore, the spinosity and unadorned faces of the interambulacral plates are both invalid for diagnostic purposes, which, along with the tube foot pore and ten interambulacra between the spiraling amb render *Westgardella* (Durham, 1993) a junior synonym of genus *Helicoplacus* (Durham, 1963).

The genus *Westgardella* as erected by Durham (1993) housed three species, *Westgardella curtisi* Durham and Caster 1963, *Westgardella firbyi* Durham 1967, and

Westgardella blancoensis Durham, 1993. *W. curtisi* was distinguished from other "Westgardellids" by plate length to width ratios of 1:1 to 3:2, prominent spines, angulate distal margins to interambulacral ridge plates, and a fusiform test shape (Durham, 1993). *W. firbyi* was distinguished form other "Westgardellids" by interambulacral ridge plate length to width ratios of 1:1 to 2:1, and no external ornamentation to plates (Durham, 1993). *W. blancoensis* was distinguished from other "Westgardellids" by interambulacral ridge plate length to width ratios of 1:1, flattened plate profile, slight angulation to interambulacral ridge plates, and fusiform theca shape (Durham, 1993). None of these characters serve to distinguish true taxa from ontogenetic or posture variations. As in *Helicoplacus,* any "Westgardellid" with an interambulacral ridge plate length to width ratio of 1:1 can be diagnosed as any of the three genera. Also, the differences in thecal shape are meaningless in a group that was capable of expansion and contraction, and therefore thecal shape change. Any variation in angulation versus spine development as well as plate aspect ratio can be explained in light of ontogeny. Therefore, there is no distinguishing between any of the three "Westgardellids," and as the generic differences do not distinguish the group from genus *Helicoplacus,* all Westgardellids are referable to *Helicoplacus* generically, and *Helicoplacus gilberti* Durham, 1963 specifically.

Waucobella nelsoni was included in the invalid Family Westgardellidae. The genus was diagnosed as having 12 interambulacral areas between branches of the curved ambulacrum, and tube foot pores between laterally adjacent cover plates. Specific diagnosis is "as for genus" (Durham, 1993). Neither of these characters are valid for diagnostic purposes. The original diagnosis of the species in Durham 1967 is far more accurate and useful, as the 1993 diagnosis seemed an attempt to shoehorn the taxon into

the invalid family Westgardellidae. In the specific diagnosis Durham (1967) noted the complexity of the ambulacrum and the predominance of spines on the distal tips of interambulacral ridge plates. Despite the invalidity of the other previously discussed species, *Waucobella nelsoni* remains a distinct species based on the complicated ambulacra. Interambulacral plates in this species are the only to have a greater length than width, and the only to have a spine at the tip of every interambulacral ridge plate, but these characteristics are trivial and may only exist in the holotype. The ambulacrum is far more complex and disparate than that of *Helicoplacus gilberti*. The reconstruction by Durham (1967, 1993) is for the most part correct, save for labeling. *Waucobella* floor plates each have three unique cover plates situated upon the distal edge. One of these is a rhombus-shaped plate that lies in a cleft between laterally adjacent flooring plates (Figure 3.36). Another is an isotropic plate contiguous with and immediately to the upper right of the rhombus shaped plate. This isotropic plate also makes contact with the flooring plate.

Above these basal plates are a series of small isotropic plates, the abundance of which was overestimated by Durham, as the row of these plates from the opposite ambulacral cover plate series interdigitates, making for the appearance of twice as many of these plates as really exists. The distal-most cover plates shown in Durham's 1967 reconstruction are the tips of these distal plates from the opposite ambulacrum.

The disparity in ambulacral morphology of *Waucobella nelsoni* is sufficient to distinguish the group from *Helicoplacus gilberti*. The group additionally shows different interambulacral ridge plates. Each terminates distally in a spine, and each is longer than

each is wide, a trait unique in the group. Together, these two differences maintain the placement of this group in a genus separate from that of the other helicoplacoids.

Polyplacus kilmeri Durham 1967 is the most enigmatic of the helicoplacoids. Represented by one relatively complete and one partial external mold upon a single slab, it was originally placed in a separate subclass to differentiate it from all other helicoplacoid genera, based on the interpretation of its unique interambulacral column construction. Durham (1967) observed that the interambulacral columns were made of a mosaic of small tessellating polygonal plates, with periodic conical projections. Paul and Smith (1984) and Durham (1993) both wrote that the ambulacral areas of this helicoplacoid were unknown. Upon closer inspection, the interambulacral columns of these helicoplacoids are identical to a typical ambulacral cover plate series found in *Helicoplacus gilberti*, comprised of a basal row of small pentagonal primary plates and pentagonal and hexagonal secondary plates. The entire test is thusly apparently comprised wholly of ambulacral columns. Durham noticed a similarity in the interambulacra of *Polyplacus* and the ambulacra of *Westgardella*, and left this as his final observation on the helicoplacoids, without elaboration as to its significance (Durham, 1993).

The existence of *Polyplacus* can be explained as the malfunction of a regulatory gene that allowed phenotypic expression of ambulacral columns in place of interambulacra. This named "species" probably represents a "hopeful monster" that nonetheless was quite successful and grew to adulthood, despite having interambulacra substituted for by non-functional ambulacra. Were it diagnosed based on the ambulacra alone, it would be considered *Helicoplacus gilberti*, and is probably derivative thereof.

The species would be less equivocal if more specimens are recovered in order to support the specific designation, but considering the similarity to other helicoplacoids, the Subclass Polyplacida is invalid.

New systematic descriptions of the class, and of *Helicoplacus gilberti*, *Waucobella nelsoni*, and *Polyplacus kilmeri* follow below.

SYSTEMATIC PALEONTOLOGY

PHYLUM ECHINODERMATA de Bruguière, 1791

Class HELICOPLACOIDEA Durham and Caster 1963

Family HELICOPLACIDAE Durham and Caster, 1966

Diagnosis - Echinoderms with a spindle to bulb shaped theca composed of left-handed spiraling interambulacral pleats composed of ridge and accessory plates, which allow for expansion and contraction of the test. Three ambulacral branches are imbedded within interambulacral pleats and extend away from a mediolateral mouth; two separated by one to thee interambulacral pleats extend toward the upper pole, and one toward the lower pole. Ambulacra are comprised of biserial floorplates and sheets of coverplates. The ambulacral groove has sutural gaps between laterally adjacent floorplates, which form compensation space for the ampullae of tube feet.

Genus HELICOPLACUS Durham and Caster, 1963

Etymology – From the Greek *helix*, spiral, and *plakos*, flat plate

Type species – Helicoplacus gilberti Durham and Caster, 1963.

Diagnosis – Helicoplacoids with differentiated ambulacra and interambulacra. Coverplates and floorplates contiguous, with two coverplate rows, and a third covering the mouth.

HELICOPLACUS GILBERTI Durham and Caster, 1963

Helicoplacus gilberti Durham and Caster, 1963, p. 821, figs. 1A-B, 1E-F; Fell and Moore, 1966, p. U112, fig. 91; Durham and Caster, 1967, p. U132, fig. 107, p. U134, fig. 109B, p. U110, fig. 110B; Durham, 1993, p. 594, fig. 3-2, p. 595, fig. 4-1.

Helicoplacus everndeni Durham, 1967, p. 96, pl. 14, fig. 1-6; Durham 1993, p. 593, figs. 2-1, 7-5.

Helicoplacus casteri Durham, 1993, p.597, Fig. 5-1, 5-3, 5-6, p. 599, 7-1.

Helicoplacus guthi Durham, 1993, p. 599, figs. 7-4, 7-6.

Westgardella curtisi Durham and Caster, 1963, p. 821, fig. 1C-D; Durham and Caster, 1967, p. U134, fig. 109A; Durham 1993, p. 593, fig. 2-2, 2-4, p. 595, fig. 4-3, p. 597, figs. 5-3, 5-4, p. 599 fig. 7-2, p. 602, figs. 8-1, 8-3.

Westgardella firbyi Durham, 1967, p. 96. pl. 14, fig. 1-3; Durham 1993, p. 593, fig. 2-3.

Westgardella blancoensis Durham, 1993, p. 598, figs. 6-6, 6-7.

Type material – Holotype, UCMP 37847; paratypes, UCMP 37844, 37849, 37854; hypotypes, UCMP 38156, 38158, 38163.

Diagnosis – As for genus.

Description - Ambulacral areas are simpler in this species than in *Waucobella nelsoni*; the lack of the single rhomb-shaped plate makes for easy diagnosis. There are also only two coverplate rows in this species (Figure 3.37A, 3.38A); presence of a third

indicates a proximity to the mouth. The primary ambulacral plates are right pentagons; directly above are two polygonal secondary coverplates for each primary coverplate. Interambulacral ridge plates have grooves along the edge of the plate, which become distorted through ontogeny as plates increase in length and occasionally form spines.

Discussion – This species shows ontogenetic variation, which in addition to plate posture, and misinterpretation of ambulacral ligament pits, coverplates, and floorplates, led to the erroneous naming of six additional species before being synonymized herein.

Etymology – Named in honor of C. M. Gilbert (Durham, 1963).

Occurrence – Lower Cambrian Poleta Formation, *Nevadella* Trilobite Zone, Westgard Pass area of the White-Inyo Mountains, Inyo County, eastern California, and Indian Springs area of Esmeralda County, western Nevada.

Genus WAUCOBELLA Durham, 1967

Etymology – Named for Waucoba Peak, White Inyo Mountains, eastern California (Durham, 1967).

Type species – *Waucobella nelsoni* Durham, 1963.

Diagnosis – Helicoplacoids with a rhombus shaped plate at the intersection of the distal corners of floorplates and proximal corners of primary coverplates. Faces of interambulacral plates are right pentagons with the acute end directed away from the animal (Figure 3.37B, 3.38B).

WAUCOBELLA NELSONI Durham, 1967

Waucobella nelsoni Durham, 1967, p. 96, fig. 1-4, 1-5, p. 99, text-fig. 1; Nichols, 1969, p. 105-106, fig. 18; Durham, 1993, p. 594, fig. 3-1, p. 595, fig. 4-2.

Type material – Holotype, UCMP14769.

Diagnosis – As for genus

Description – The ambulacral areas are far more complex than those of *Helicoplacus* gilberti and *Polyplacus kilmeri,* which makes this genus and species recognizable at a glance.

Discussion - The ambulacral areas in *Waucobella nelsoni* differ most notably by the sheer number of ambulacral covering plates. The simplest diagnostic tool is the single rhombus-shaped plate at the intersection of the flooring and covering plates. Each primary coverplate has three polygonal secondary coverplates attached to the distal edge, and distal to these are yet two additional rows of polygonal plates. The fundamental repetitive unit of the ambulacrum has some variation in plate size and shape from segment to segment, but relative plate number and position remains relatively constant.

The interambulacral plates of this helicoplacoid are sufficiently different from those of *Helicoplacus gilberti* that they can also be used as a diagnostic tool. Each interambulacral plate is a uniform right pentagon, with the pointed edge directed away from the axis of symmetry of the theca.

Durham (1967, 1993) considered the ambulacra of this specimen to reach the tip of the upper pole. Some juvenile spindle-shaped *Helicoplacus gilberti* specimens also show ambulacra that reach the upper pole, whereas ambulacra in adult specimens do not. This suggests that insertion of new ambulacral plates at the end of the ambulacrum ceases

at a point in ontogeny, and interambulacral plates continue to be inserted above it. As the ambulacra appear to reach the upper pole in *Waucobella,* it is likely either a juvenile, or a neotenic specimen. Because this character varies through ontogeny in *Helicoplacus gilberti*, and because there is only a single specimen of *Waucobella nelsoni* upon which to draw comparisons, this is not a useful taxonomic tool.

The only truly unique distinguishing characteristics are the extra rhomb-shaped ambulacral plate, extra ambulacral cover plate rows, and diagnostic interambulacral ridge plates. Further collection and study will hopefully further validate this genus and species. Two recently collected specimens, one by the author and deposited in the TMM, and another by Stephen Q. Dornbos and deposited in the LACMNH, may represent fragments of this species, but are too incomplete to diagnose.

Etymology – Named in honor of Clemens A. Nelson (Durham, 1967)

Occurrence – The unique holotype specimen is from the Lower Cambrian Poleta Formation, *Nevadella* Trilobite Zone, Westgard Pass area of the White-Inyo Mountains, Inyo County, eastern California.

Genus POLYPLACUS Durham, 1963

Polyplacus kilmeri Durham, 1967, p. 96, pl. 14, fig. 1-1, 1-2.

Etymology – From the Greek *polu*, many, and Greek *plakos*, flat plate

Type species – Polyplacus kilmeri Durham, 1967

Diagnosis – Helicoplacoids with interambulacra composed of fused basal plates in the shape of a right pentagon, and twice as many distal polygonal plates.

POLYPLACUS KILMERI Durham and Caster, 1963

Durham, 1967, Plate 14, Figures 1, 2.

Type material – Holotype, UCMP 14767; paratype, 14768.

Diagnosis – As for genus

Description – The interambulacra are composed of myriad smaller plates. Durham (1993) noted a similarity to *Waucobella* ambulacra, but the shape and organization is identical to that of *Helicoplacus gilberti*. The interambulacral ridges are fused, and are organized into knobs.

Discussion – Were this specimen diagnosed solely on the basis of its interambulacra, it would likely be considered a subspecies of *Helicoplacus gilberti*. The test is composed of ambulacra, but these do not appear functional, as they are fused at the point of commissure. "Normal" ambulacra do not appear, but it is likely that an ambulacrum would not be distinguishable from a similarly plated interambulacral ridge. This specimen likely represents a developmental oddity, or "hopeful monster."

Etymology – Named in honor of F. H. Kilmer (Durham, 1967)

Occurrence – The unique holotype specimen is from the Early Cambrian *Nevadella* Trilobite Zone, Poleta Formation of the Westgard Pass area of White-Inyo Mountains, Inyo County, eastern California.

Evolutionary Relationships

In the writings of Durham and Caster (1963, 1966) and Durham (1964, 1967, 1993), the theme repeats that helicoplacoids are not the ancestral echinoderm as they occur in beds that include *Eocystites* (later renamed *Gogia*; see chapter herein) and a

possible edrioasteroid (which the author has found no evidence of). Echinoderms were then presumed to have had a long Precambrian history (Durham, 1964), as in the Early Cambrian there existed three morphologically disparate echinoderm groups. It was suggested, however (Durham and Caster, 1966), that helicoplacoids might represent a case of the ancestral ambulacral condition, in that triradiate symmetry can easily be modified to the more familiar echinodermal pentameral condition by the addition of two ambulacral areas. After the discovery of helicoplacoids, two separate groups of papers discussed this possibility.

The enigmatic triradiate fossil *Tribrachidium heraldicum* of the Upper Ediacaran soft-bodied fossil assemblage from the Flinders Ranges of South Australia was noticed to have a Y-shaped mouth and "bristles" resembling tube feet, which was taken of evidence of echinodermal affinities (Glaessner and Wade, 1966). Paul (1979) wrote that on the basis of his observation of figures only, *Tribrachidium* was probably an echinoderm. These conclusions are most probably based o the original assertions of Durham and Caster (1963) that the ancestral echinoderm was triradiate, which spawned a search for a Precambrian triradiate domal animal. Gehling (1987) discussed the occurrence of a contemporary and co-occurring pentameral Upper Ediacaran soft-bodied fossil from the Flinders Ranges of South Australia. The fossil, named *Arkarua adami* was hypothesized to represent a clade of echinoderms excluding the triradiate forms *Tribrachidium* and *Helicoplacus*, suggesting that echinoderm history predated the Ediacaran, and that by the occurrence of the Ediacaran forms, the diversification of triradiate and pentameral forms had already occurred. This is very unlikely, as the only commonality shared by true echinoderms and the Ediacaran forms is symmetry. Ediacarans have none of the other

echinoderm synapomorphies, namely a water vascular system, and a skeleton composed of stereom. The tree proposed by Gehling (1992) requires the independent development of stereom in both clades, which is unlikely.

Furthermore, pentamery itself is derived from the development of the echinoderm skeleton in the evolutionary pathway proposed by Nichols (1967, 1969). At some point in ontogeny, echinoderms pass through a stage in which there is a single ring of plates, which give rise to the pentameral echinodermal body. The presence of five plates results in a ring in which there is no plane of weakness (Figure 3.39); for example a ring composed of four plates would have a plane of weakness that passes through the sutures of two sets of plates, while a plane passing through one suture in a pentameral ring would intersect the center of a plate element on the opposite side of the ring. Therefore pentamery must have existed in the ancestral echinoderm before the development of a skeleton, which likely followed as a response to the advent of predation. This again makes Gehling's bifurcation of soft-bodied forms unlikely, as pentamerism predates skeleton development, which forces the unlikely situation that triradiate forms would have developed identical stereom skeletons.

Hotchkiss (1998) proposed an evolutionary scheme in which an initial uniradiate ancestor gave rise to a triradiate form through adherence to Bateson's rules of symmetry, involving supernumerary appendage duplication. The triradiate echinoderm then restored bilateral symmetry by developing two additional ambulacra, resulting in the more familiar pentameral symmetry, leaving helicoplacoids as an evolutionary intermediate (Hotchkiss, 1998). These theories were modeled from the oral frame of the holotype

specimen of *"Stromatocystites" walcotti*, without any evidence of the helicoplacoid oral frame, and without further examples of edrioasteroid oral frames as evidence.

The more likely scenario is that helicoplacoids are derived from pentameral skeletized ancestors. Mooi and David (1997) and David et al. (2000) presented cladograms in which pentamerism is ancestral to all echinoderms, in support of this thesis. Sumrall (2000) wrote of the propensity for echinoderms to loose ambulacra, providing a means by which helicoplacoids became triradiate. Juvenile echinoderms have only two lateral ambulacral branches, designated BC and DE for a 1-0-1 ambulacral arrangement. Development of the A ambulacrum follows, resulting in a 1-1-1 arrangement, followed by bifurcation of the lateral branches, giving the familiar 2-1-2 arrangement (Sumrall, 2000).

The relationship between an echinoderm group with three ambulacra and another with five ambulacra is easily resolved; adding or reducing two ambulacra gives the opposite topology. Many early echinoderm groups, including edrioasteroids and eocrinoids, share an ambulacral morphology that is best described as "2-1-2" rather than pentamerous (Sprinkle, 1973). The mouth has three ambulacra leading away from it proximally, two of which branch more distally, to give the more familiar pentameral arrangement. Furthermore, this establishes bilateral symmetry, with the plane of symmetry bisecting the A ambulacrum. This triradial proximal amb symmetry is more pronounced in some groups; for example an as-of-yet undescribed eocrinoid from the Middle Cambrian Burgess Shale of British Columbia, Canada, upon which the ambulacra do not branch until they reach the edge of the oral surface (James Sprinkle, personal communication). Later echinoderm groups, including extant taxa, have lost the 2-1-2

pattern, which has been altered to a true pentameral arrangement, as in the Eleutherozoa ("1-1-1-1-1")(Sumrall, 2000). Given that helicoplacoids are derived from a 2-1-2 ancestor, it is necessary that at least two ambulacra become reduced and eventually lost in the evolution of the helicoplacoid bauplan.

Camptostroma is a close to the ancestral echinoderm condition as exists in the fossil record, a premise borne out by several systematic studies (Paul and Smith, 1984 [with the exception of the helicoplacoid position]; Guensburg and Sprinkle, 1994; Sumrall, 1997; Mooi and David, 1997). The following series of transformational steps are capable of transforming a generalized *Camptostroma*-like edrioasteroid into the highly derived helicoplacoid bauplan.

Camptostroma has A, B, D, and E ambulacra that are curved counter-clockwise (dextral) distally, and a C ambulacrum that curves clockwise (sinistral) (see chapter herein on *Camptostroma*.) This ambulacral orientation created an enlarged CD interray, as the C and D ambulacra and associated terminal plates were pointed toward one another, inserting plates in opposing directions. The aberrantly curved C ambulacrum is then probably associated with the positioning of the anal pyramid in this interray, and is therefore probably ancestral in Echinodermata, as all early echinoderms (except *Helicoplacus*) show an anal pyramid in the CD interray. While *Camptostroma* increased its ambulacral surface area by extending the thecal surface into the water column, an alternative means of doing so is by ambulacral spiraling. While *Camptostroma* did this to some decree with distal curvature, other edrioasteroid taxa specialized in elongation of the ambulacra by spiraling. For example, the edrioasteroid taxa *Lebetodiscus*, *Foerstediscus*, and *Streptaster* (Bell, 1976) have ambulacra that spiral uniformly in the

counter-clockwise direction. In order to continue elongation of the theca, the curved ambulacra have caused the animal to grow upward into the water column, away from the sediment-water interface. Since the ambulacra and adjacent interambulacra experience plate insertion at the tips of each counter-clockwise ambulacrum, the resulting thecal orientation is a left-handed spiral (Figure 3.40).

A similar better-developed convergent case is found in the diploporan *Gomphocystis tenax*, although this taxon shows entirely clockwise-curving ambulacra. The animal has an elongate theca which is wound into a right-handed spiral, as a result of the opposite ambulacral curvature (Figure 3.41) (Beaver at al., 1968). Bather (1900) wrote that this was an adaptation to increase surface area dedicated to feeding. The animal is convergent with the helicoplacoid bauplan, with the additional analogy of a bulb-shaped theca.

Helicoplacoids likely arose by growth into the water column as in *Gomphocystis* from a *Camptostroma*-like ancestor with a similarly aberrantly curving C ambulacrum. Since ambulacrum C curved in the opposite direction, it was lost, leaving four uniformly curving ambulacra. In order to maintain bilateral symmetry, either the D or E ambulacrum was lost. Considering the close proximity of the upward-spiraling ambulacra, E is probably the other reduced ambulacrum, which leaves the more closely spaced ambulacra B and D, in addition to A. The result is a triradiate edrioasteroid with uniformly counter-clockwise (dextral) ambulacral tips.

At some point in the developmental history of helicoplacoid ancestors, the epispire-bearing oral surface was greatly reduced, and replaced by the pleated aboral surface of *Camptostroma*, likely in response to a change in respiratory mode to cloacal

pumping. The corrugations would have allowed the theca to expand and contract, filling respiratory trees. The result at this point in development is a triradiate edrioasteroid with pleats between the three ambulacra, and the anus located within the greatly reduced perforate extraxial area around the mouth.

The theca then continued developing an elongate theca along the axis through the mouth and aboral surface, growing into a left-handed spiral. Development of a bulb-shape resulted from extensional growth of already inserted plates, which proved advantageous by further elongating the ambulacra. The end result of this stage is a large bulb-shaped echinoderm with the mouth at the summit three trailing ambulacra, adjacent pleated interambulacra, and an anus adjacent to the mouth.

The close proximity of the mouth and anus then forced the mouth to "migrate" down the A ambulacrum, taking with it the additional two ambulacra, until the mouth reached a mediolateral position, away from the anus. The fact that the ambulacra do not extend to the upper pole and anus in adults is a consequence of potential befouling of the area immediately adjacent to the anus. The result at this point is the helicoplacoid bauplan, with the anus at the summit, aboral pad at the lower pole, mouth mediolateral, and pleated interambulacra between ambulacra (Figure 3.42).

The author acknowledges two possible variations of this developmental scheme. The steps resulting in pleats between ambulacra and reduction to three ambulacra and initiation of spiraling growth could be concurrent, or in the opposite order. Also, the greatly reduced number of interambulacra between the upper branches of the ambulacrum (two) suggests that these may be the D and E ambulacra, which both curve counter-clockwise in *Camptostroma*, and are closer together than the D and B ambulacra

would be. If this were the case, the anus would lie to the left of the D ambulacrum, rather than between the two upper ambulacra, as is the case in the above scheme. It is possible that the anus migrated, as in the case of irregular echinoids (Wagner and Durham, 1966), to take the position formerly occupied by the mouth. It seems that either of these scenarios are equally likely.

Important evolutionary cues derived from this developmental scheme include the homology of helicoplacoid pleated interambulacral areas and the pleated aboral skirt of *Camptostroma*, and homology of the aboral attachment pads in these taxa. Development of the helicoplacoid bauplan requires counter-clockwise curved ambulacra, and loss of the C and either the D or E ambulacrum. Helicoplacoids then do not represent a case of neoteny, as the ambulacra must have been curved distally, which occurs only later in the growth of edrioasteroids.

Conclusions

1. Helicoplacoid systematics were misinterpreted by previous authors. Nine species of helicoplacoid are reduced to three, *Helicoplacus gilberti*, *Waucobella nelsoni*, and *Polyplacus kilmeri*, which probably represents a "hopeful monster."

2. Helicoplacoids were capable of expansion and contraction, as well as a third intermediate posture, which exposed the superior faces of the interambulacral ridge plates. These variants in posture served to confound previous systematic studies. Helicoplacoids expanded the theca and respired by cloacal pumping.

3. Helicoplacoids were attached to skeletal debris when available, and to microbial mats when necessary. Previous authors considered helicoplacoids to have inserted the lower pole into soft substrates.

4. Helicoplacoids are reassessed as highly derived triradiate echinoderms, sharing stereom, modified pentamery, and the homologous skeletal regions as outlined in the EAT Theory with ancestral stock.

5. Helicoplacoids grew by plate addition and plate growth. New plates were added at plate generative zones at either pole.

6. The mouth was situated mediolaterally, receiving food particles and debris collected by the tube feet and passed into the ambulacra, which then passed food particles to the mouth. Helicoplacoids had a gut for processing the organic material from the rain of sedimentary particles, which likely emptied from a pyramid-lacking anus at the upper pole.

7. Helicoplacoids were derived from pentameral *Camptostroma*-like ancestors, which became triradiate and wound into a left-handed spiral as a consequence of increasing ambulacral length.

8. Helicoplacoid aboral surfaces and interambulacra are homologous to the aboral attachment pad and pleated skirt, respectively, of *Camptostroma*.

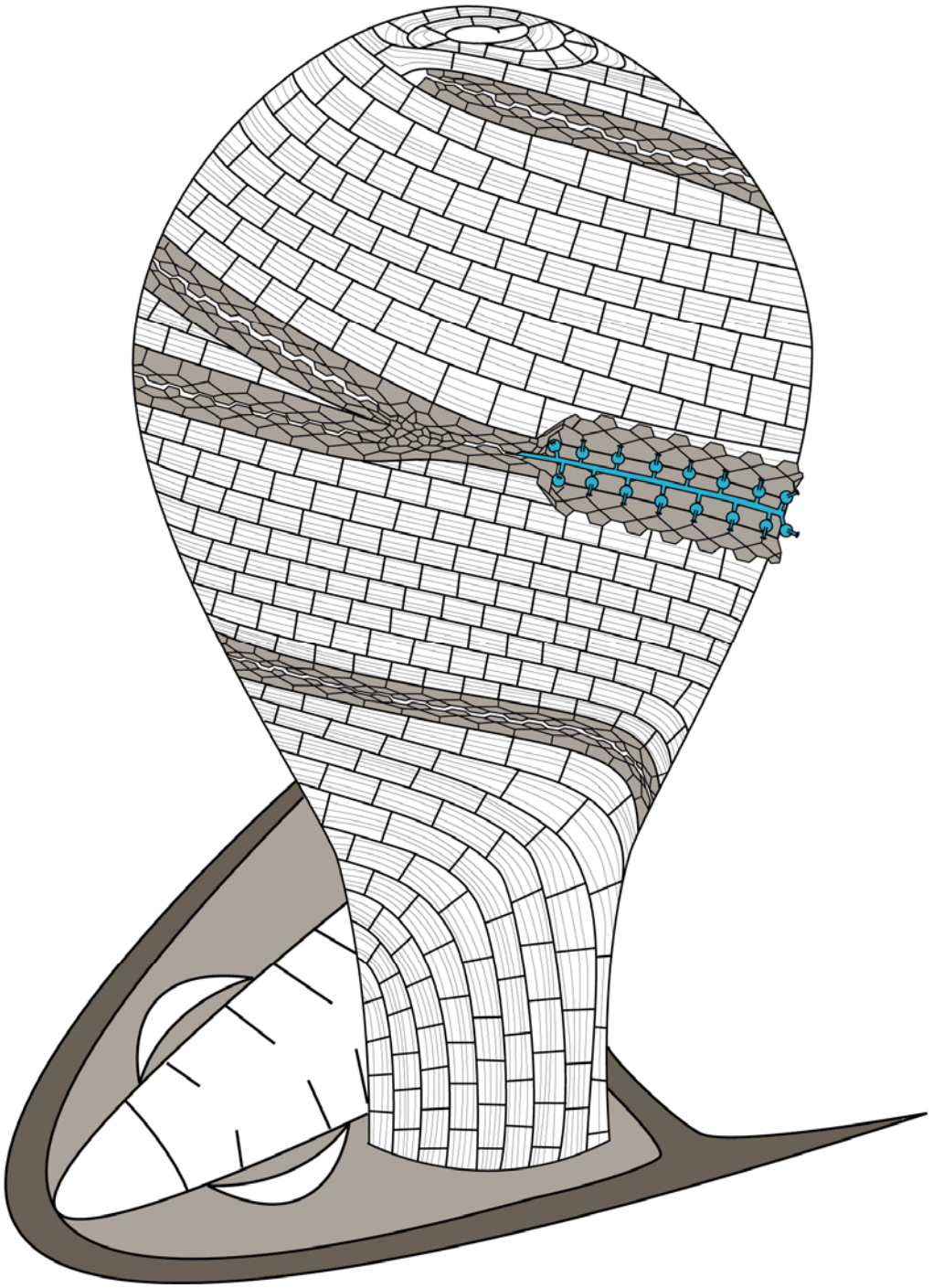


Figure 3.1. Reconstruction of helicoplacoid, attached to the cephalon of a *Nevadella* trilobite. Ambulacral cover plates (gray) are opened immediately adjacent to the mouth, exposing the water vascular system (blue). The specimen this reconstruction was modeled after is 50 mm tall.

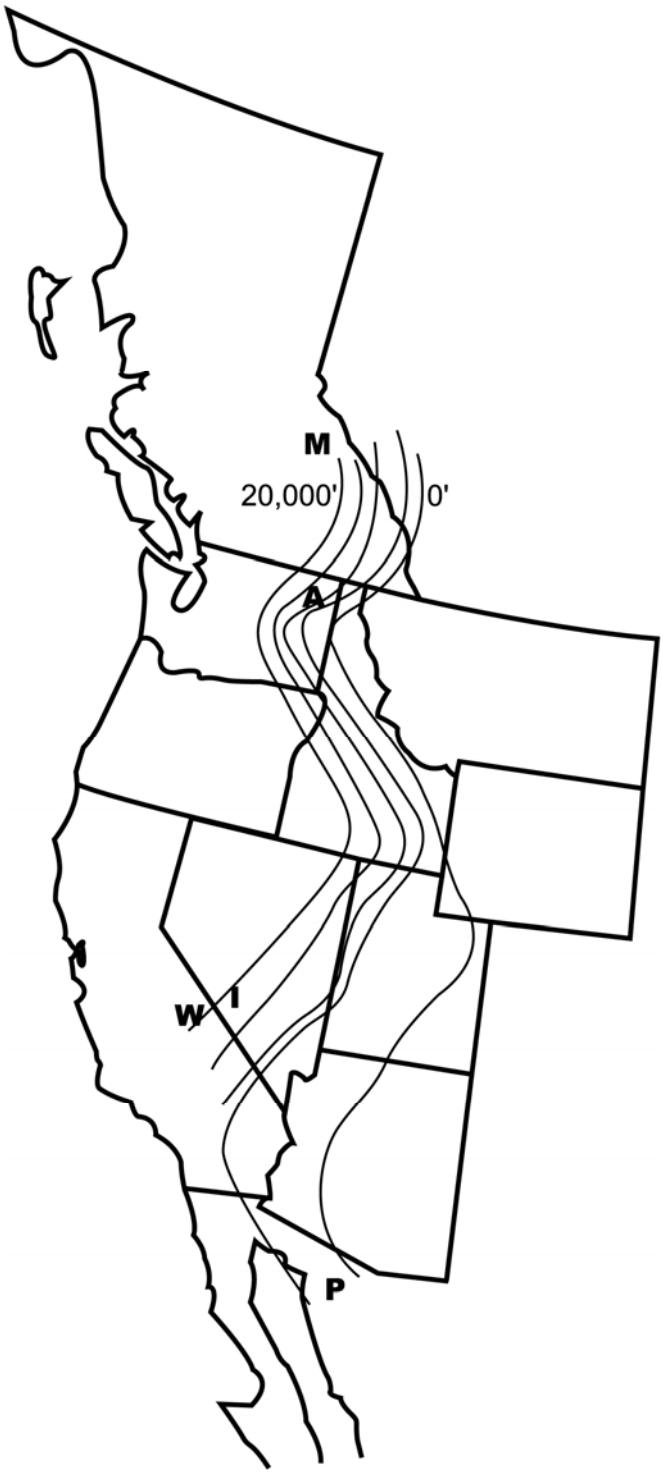


Figure 3.2. Early Cambrian helicoplacoid localities. Isopach contours are 5,000’ (1515 m) and indicate thickness of Late Proterozoic and Lower Cambrian rocks. Map modified from Stewart (1970). M is the Mural Formation locality in British Columbia, Canada; A is the Addy Quartzite in Addy, Washington; I is the upper member of the Poleta Formation outcrop in the Indian Springs area; W is the upper Poleta outcrop in the White-Inyo Mountains; and P is the Proveedora Hills locality in Sonora, Mexico.

Figure 3.3. Upper Poleta Formation, Lower Cambrian. Locality UT TMM 2031, Westgard Pass, White-Inyo Mountains, Inyo County, eastern California. The author collected at this locality during the summers of 2001-2005. N. B. McCulloch also collected here in 1967, amassing a collection accessioned by the USNM. Rock hammer for scale.

Figure 3.4. Upper Poleta Formation, Lower Cambrian. Locality UT TMM 2041, Indian Springs Canyon, Montezuma Range, Esmeralda County, western Nevada. The author collected at this locality during the summers of 2002-2005. Author under tree for scale.

Figure 3.5. Addy Quartzite, Lower Cambrian. Locality UT TMM 2042, Addy, Stevens County, northeastern Washington. The outcrop forms the small tree-covered hill in the left of the picture, which is on the property of Northwest Alloys. The author collected here in July of 2003.

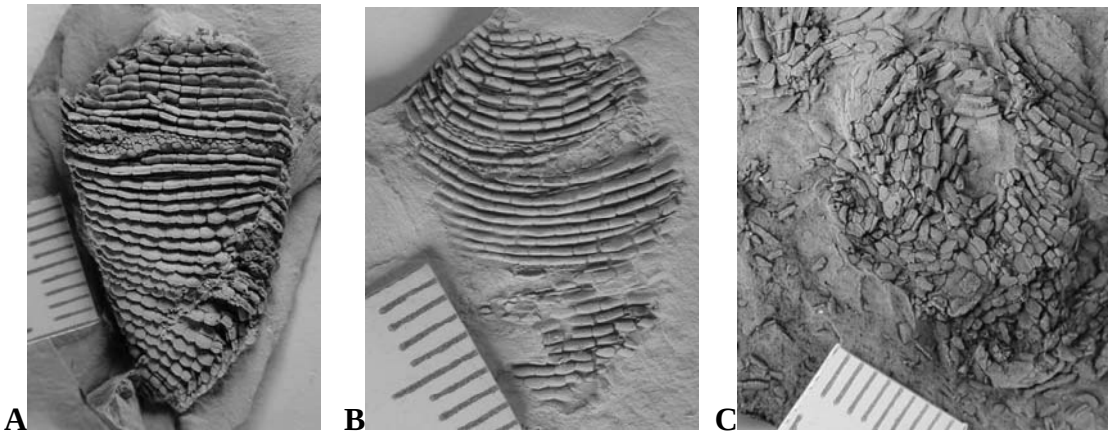


Figure 3.6. Helicoplacoid taphonomic types of Dornbos and Bottjer, 2001. A belongs to group one, which is characterized by little to no disarticulation; B belongs to group two, which is characterized by partial disarticulation; C belongs to group three, which is characterized by almost complete disarticulation (Dornbos and Bottjer 2001).

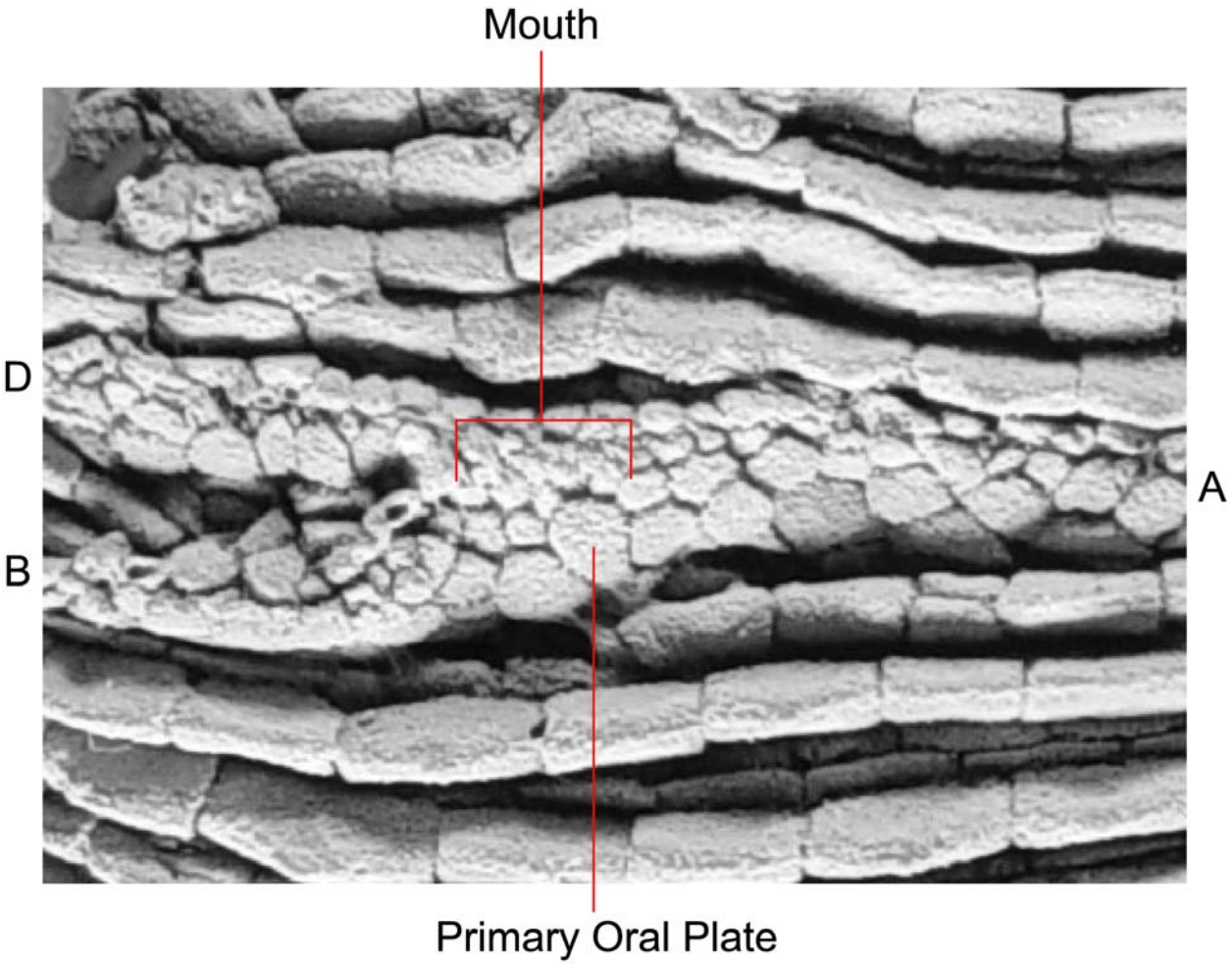


Figure 3.7. Helicoplacoid mouth, specimen UT TMM 2041TX1a. The single primary oral plate indicates that the area below the mouth is either the AB or DA interray. Considering the spacing and symmetry of the ambulacra, it is most likely that the down-going ambulacrum is A. Field of view is 8 mm across.

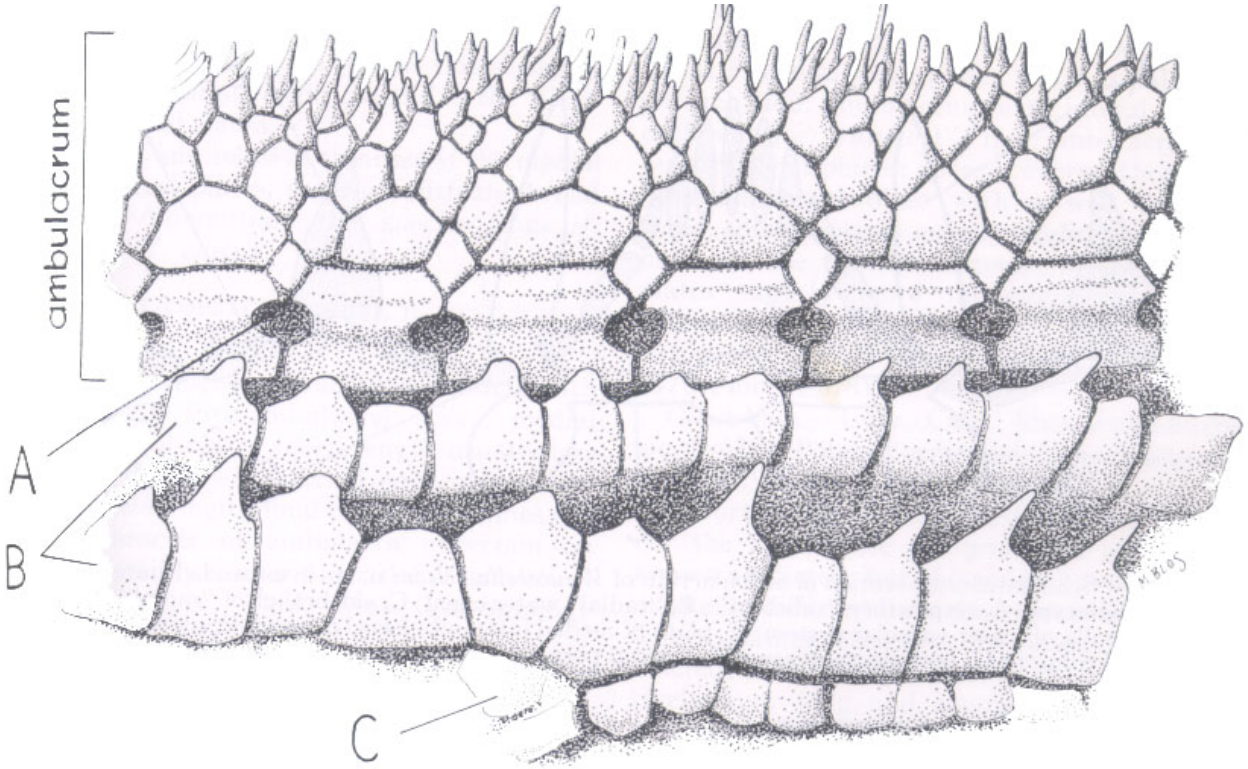


Figure 3.8. Ambulacral reconstruction of *Waucobella nelsoni* Durham, 1967. A is a sutural pore, the Bs are interambulacral ridge plates, and C is an interambulacral accessory plate. Durham misinterpreted the sutural-pore bearing plates as floor plates. Figure is modified from Durham, 1967 (Text-Figure 1, pg. 100).

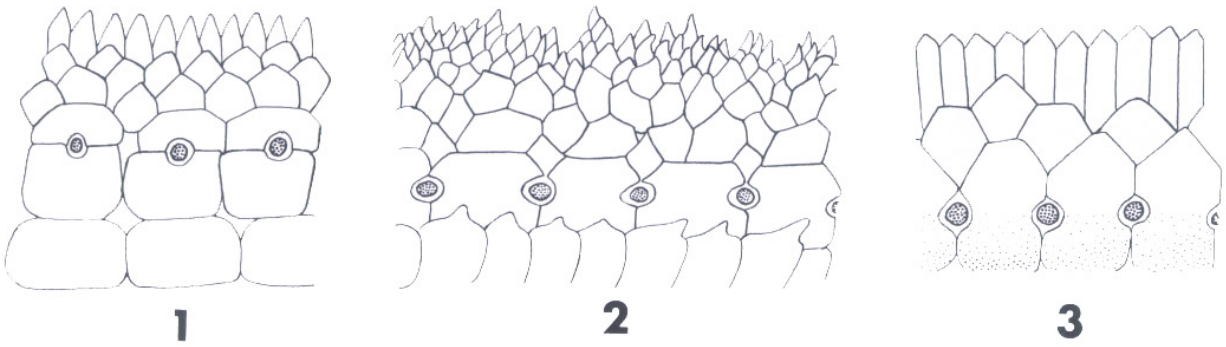


Figure 3.9. Helicoplacoid ambulacra as reconstructed by Durham (1993). 1 is *Helicoplacus*, 2 is *Waucobella nelsoni*, and 3 is "*Westgardella*." Figure is taken from Durham, 1993 (Figure 4, pg. 595).

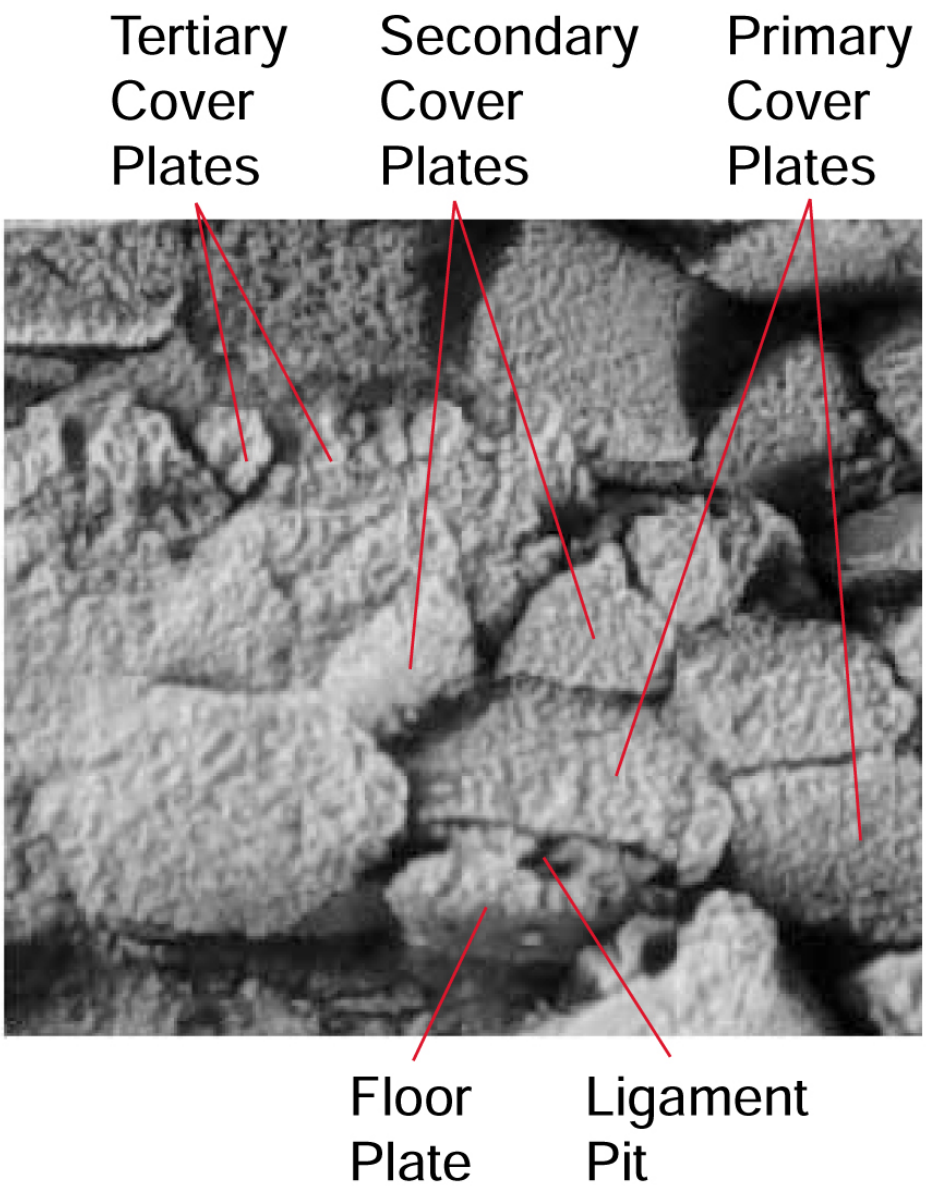


Figure 3.10. Labeled helicoplacoid ambulacrum, specimen UT TMM 2031TX1. Ligaments closed the ambulacral cover plates, which are arranged into primary, secondary, and tertiary rows. Field of view is 4 mm across.

Figure 3.11. Helicoplacoid floor plates (left) and primary cover plates (right), misidentified by Durham (1993) as the primary and secondary basal rows of cover plates (Figure 5-4, g. 597). Floor plate sequence is 7.5 mm in height.

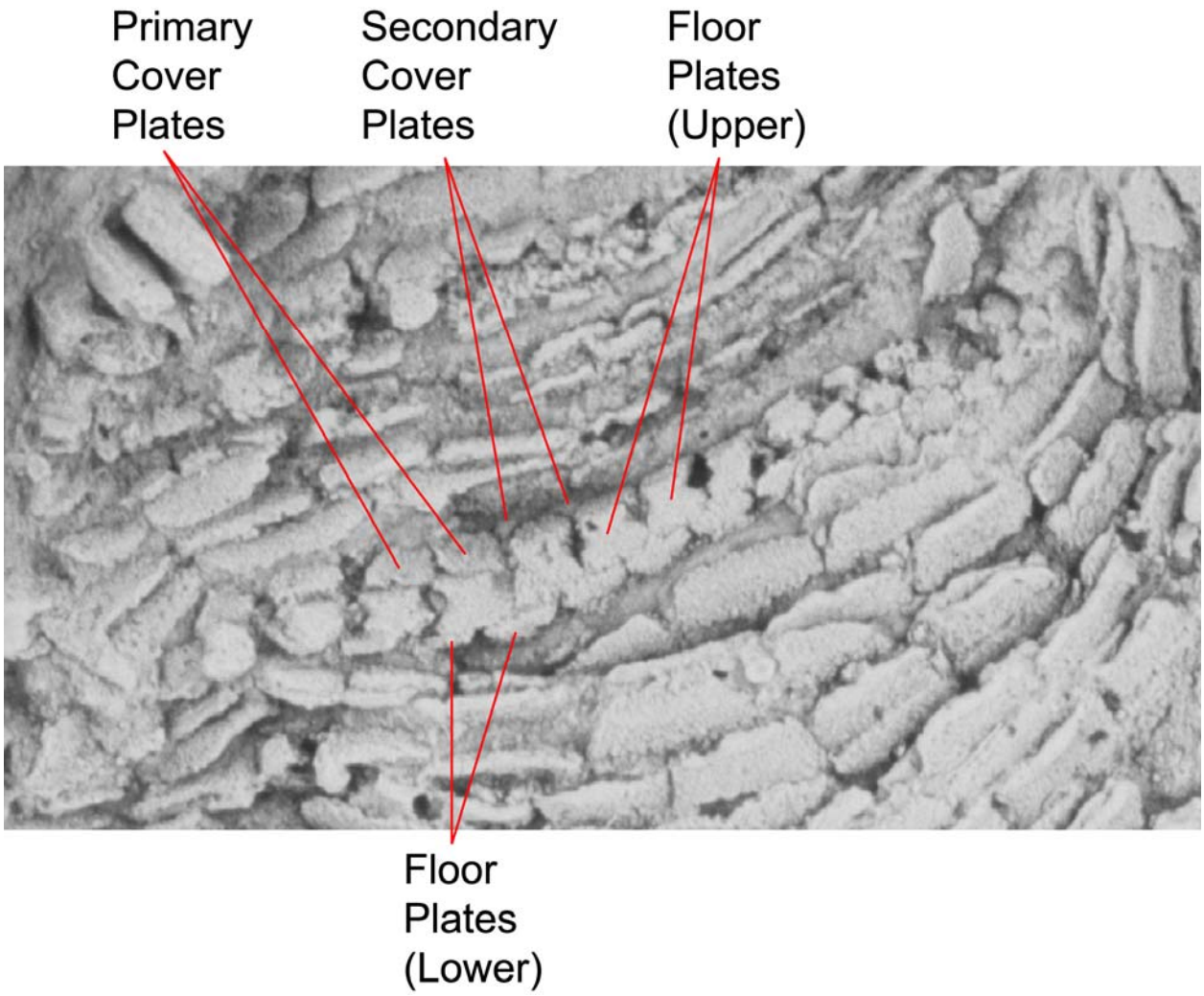


Figure 3.12. Helicoplacoid floorplates, LACMNH 17529. The mouth is toward the left; the terminus of the ambulacrum is toward the right. Note arrangement of floor plates relative to cover plates, and the biserial nature of the floor plates. "Upper" and "Lower" in reference to the floorplates is relative to the upper and lower poles. Field of view is 10 mm across.

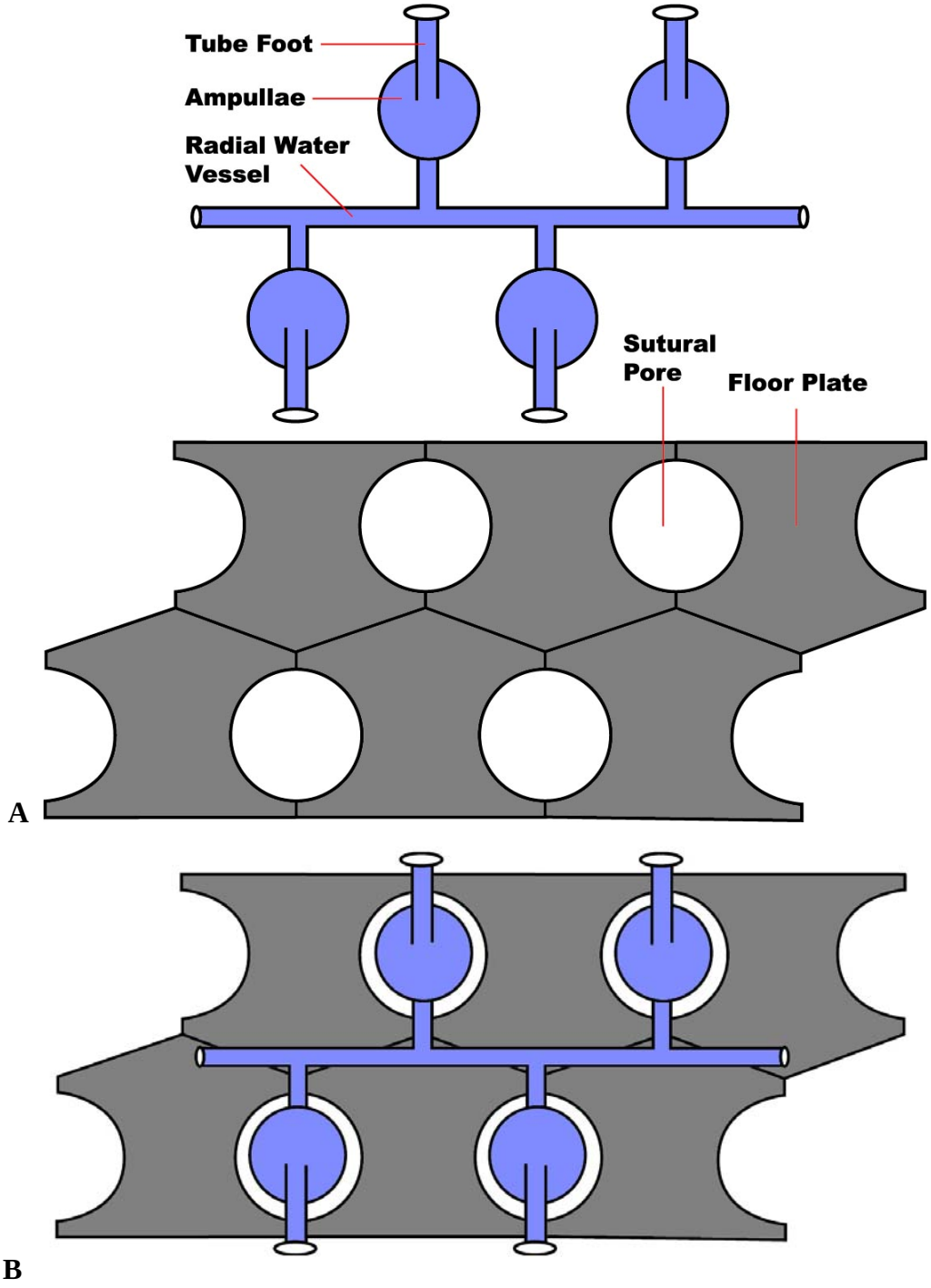


Figure 3.13. Reconstruction of interior of helicoplacoid ambulacrum with the cover plates removed. A shows the water vascular system separate from the skeletal floor plates; B shows the two systems overlain. View is from above, sutural pores are exaggerated in size to better show relation to ampullae.

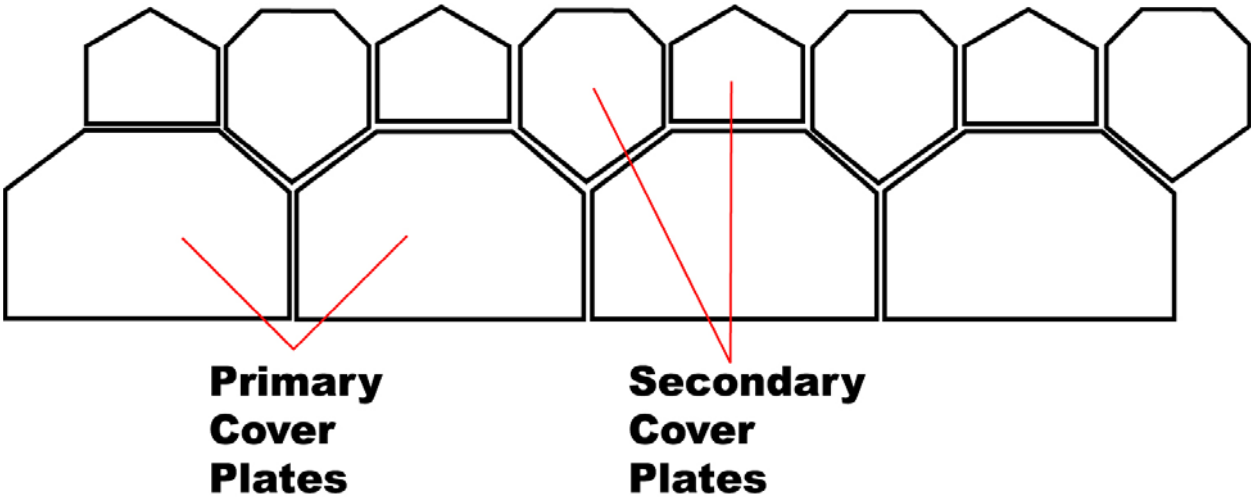


Figure 3.14. Cover plate schematic of *Helicoplacus gilberti*.

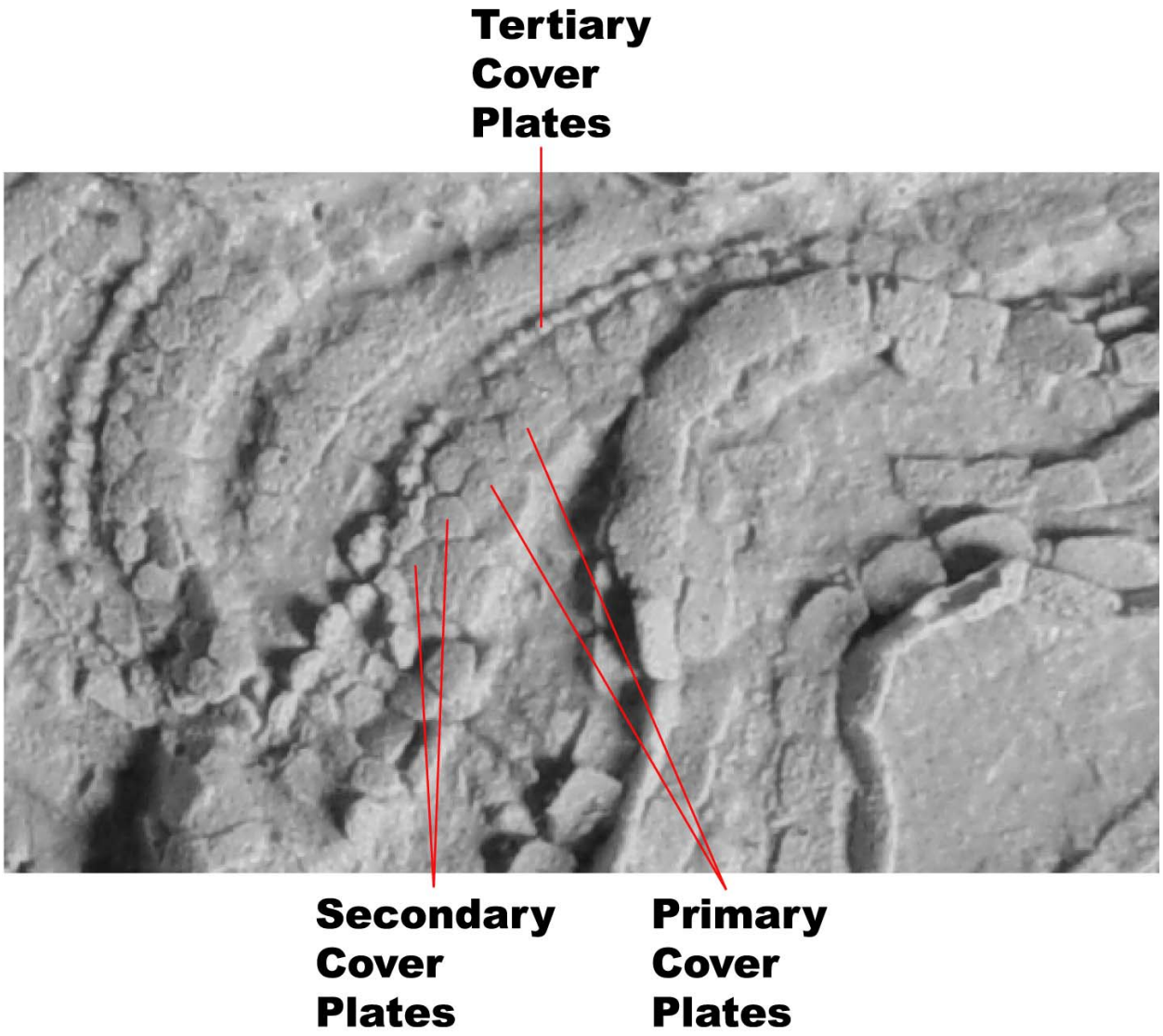


Figure 3.15. Labeled ambulacral cover plates. Specimen UCMP 38164.

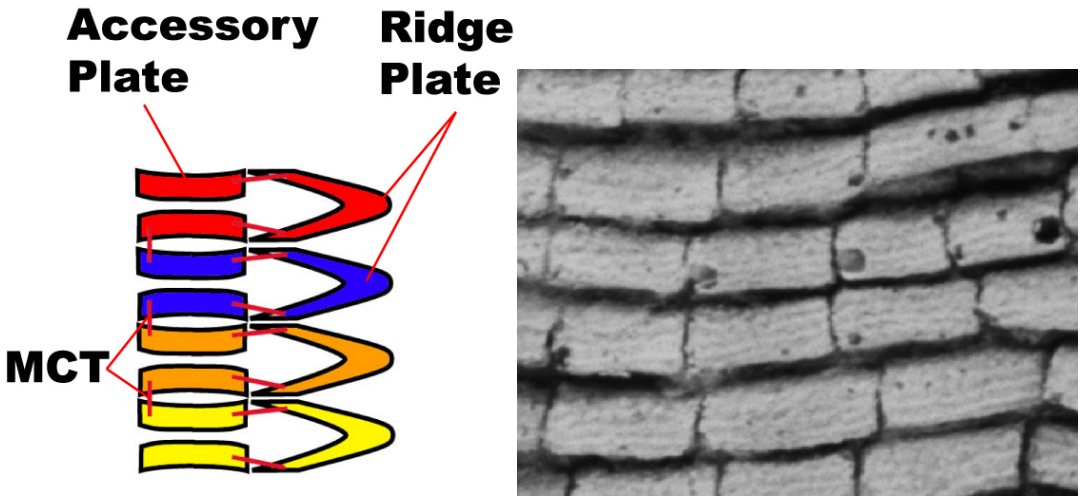


Figure 3.16A. Contracted helicoplacoid interambulacral reconstruction in cross section. Colors are to aid in following the expansion of each interambulacrum through Figure 16c. Photograph of UCMP 37847 showing this posture; field of view of photograph is 4 mm across; “MCT” is an acronym for “Mutable Collagenous Tissues.”

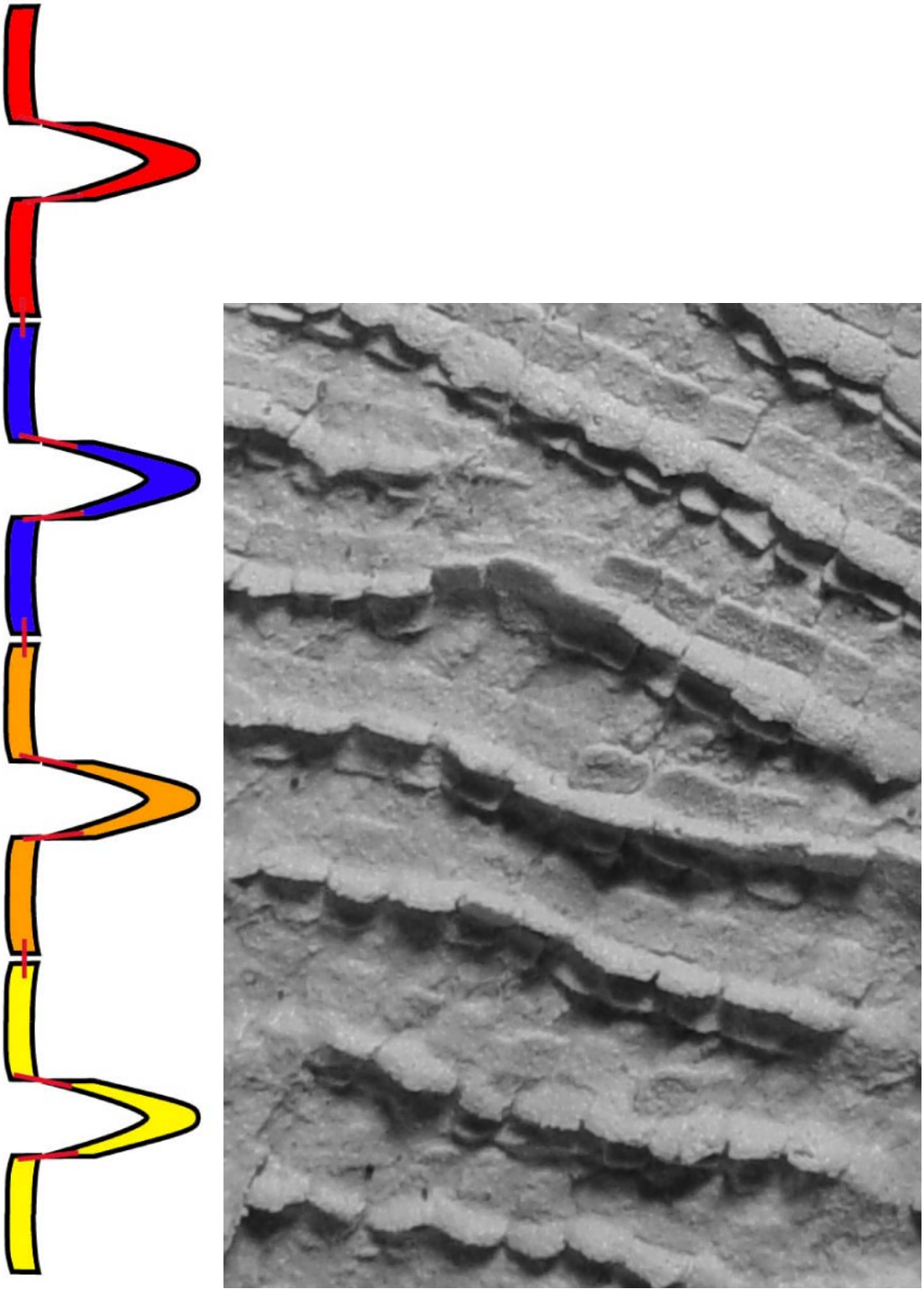
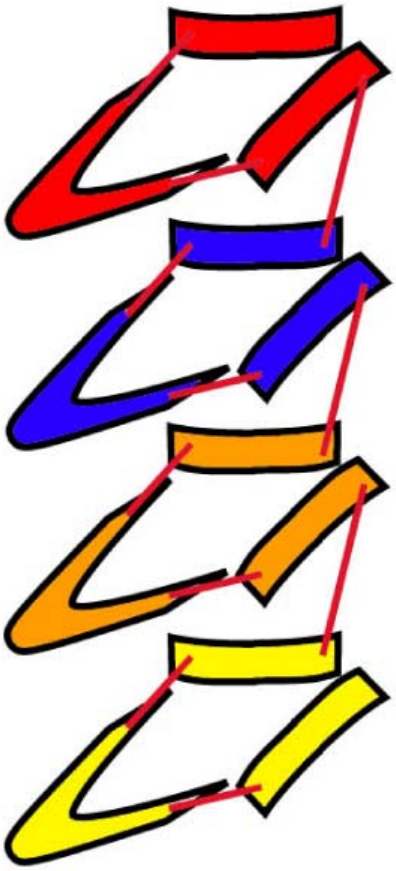


Figure 3.16B. Expanded helicoplacoid interambulacral reconstruction in cross section. Photograph of UCMP 38164 showing this posture; field of view of photograph is 22 mm in height.



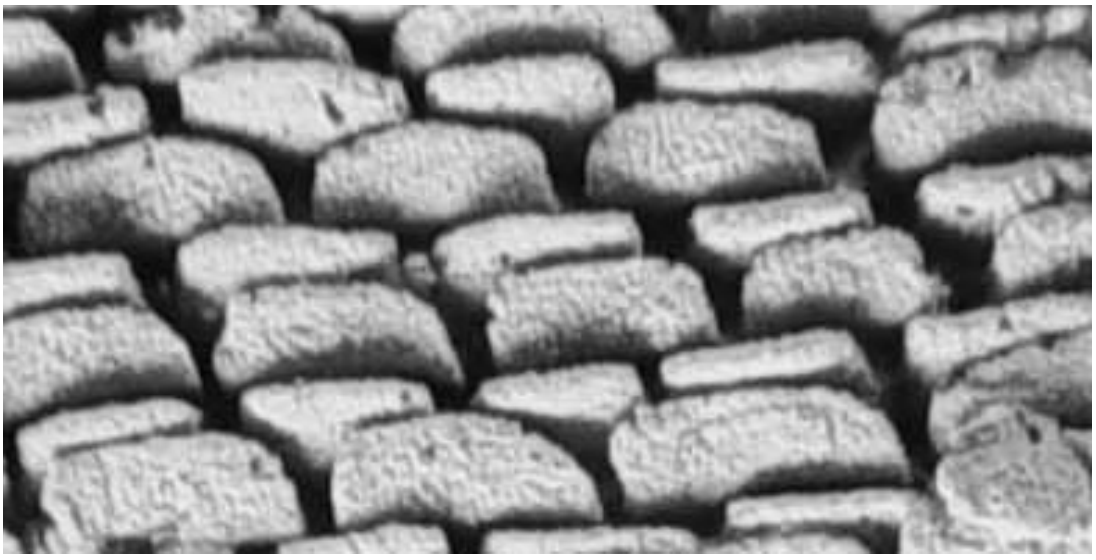


Figure 3.16C. Semi-expanded helicoplacoid interambulacral reconstruction in cross section. Photograph of interior of UT TMM 2041TX2b showing this posture. Note that rows of successive plates show either the edge or the face of the interambulacral accessory pates. Field of view of photograph is 5 mm in height.

Figure 3.17. Helicoplacoid showing well-developed interambulacral ridge plate spines. Portion of a metric ruler for scale. Unnumbered LACMNH specimen.

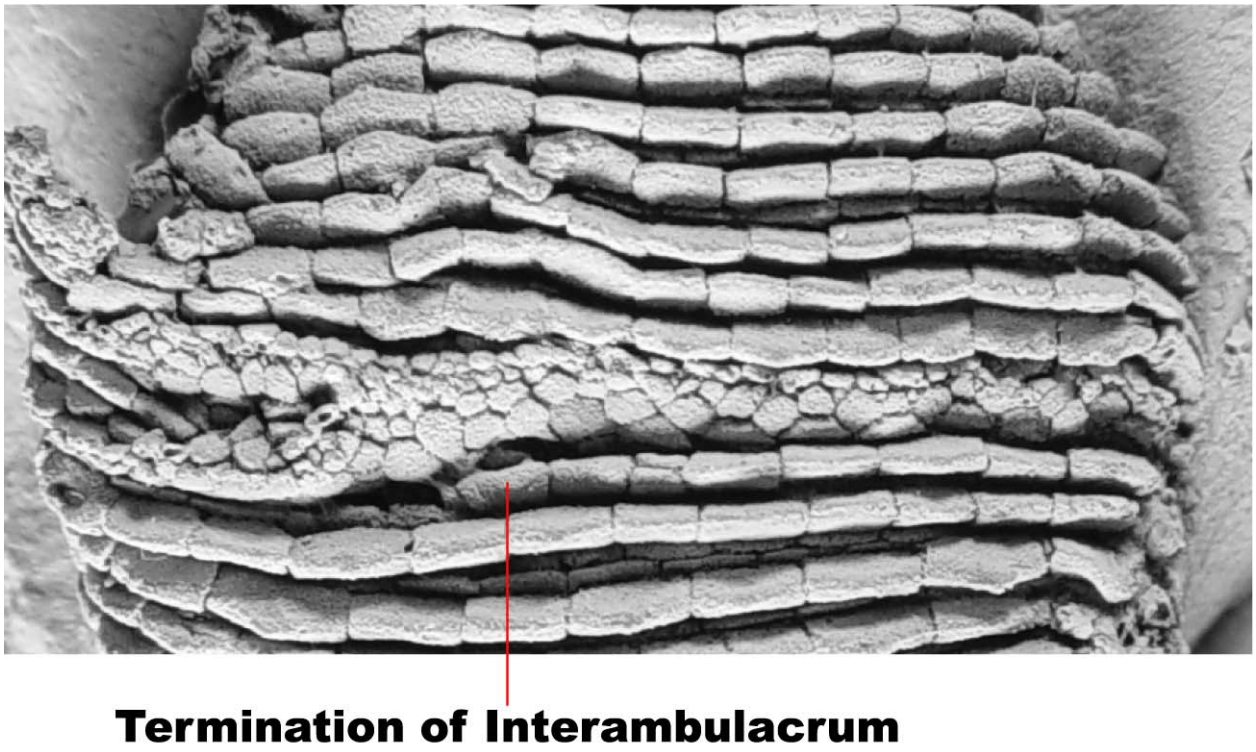


Figure 3.18. Termination of interambulacral ridge immediately below mouth. UT TMM 2041TX1a; field of view is 18 mm across.

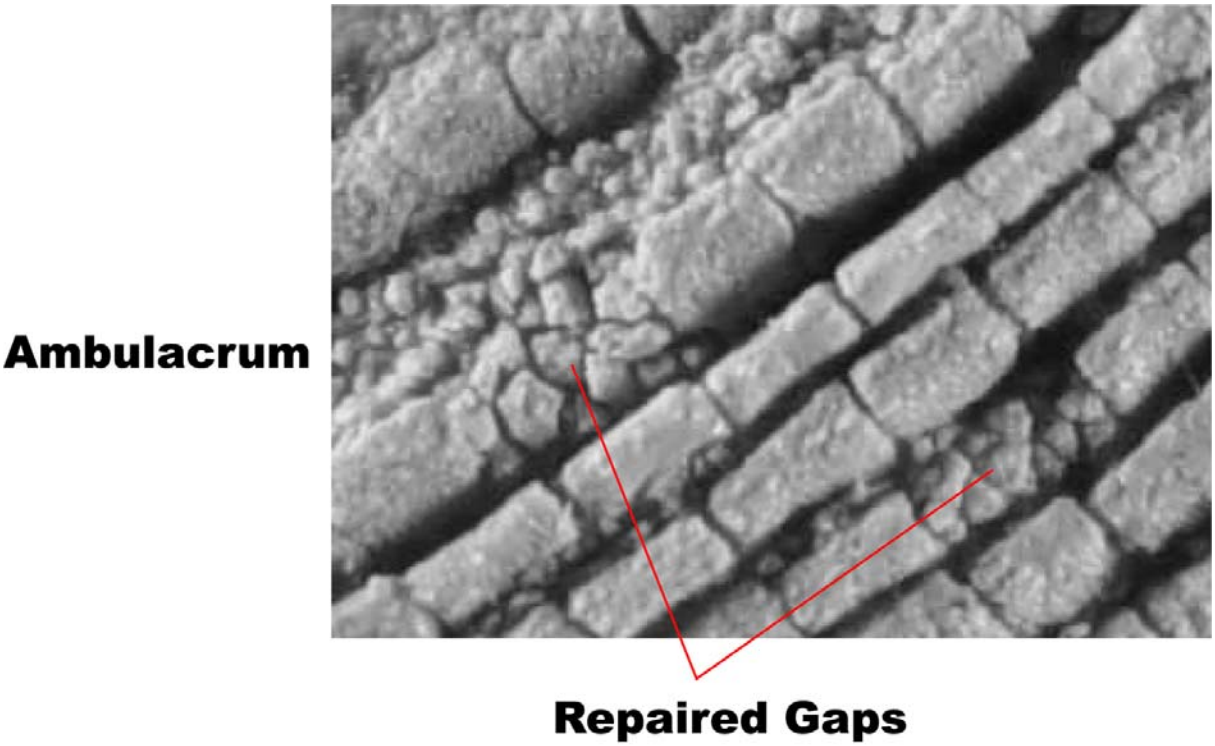


Figure 3.19. Missing interambulacral ridge plates, repaired by insertion of new plates. Durham (1993) interpreted these as the hydropore and gonopore. Field of view is 4 mm in height; photograph is of UCMP 38158.

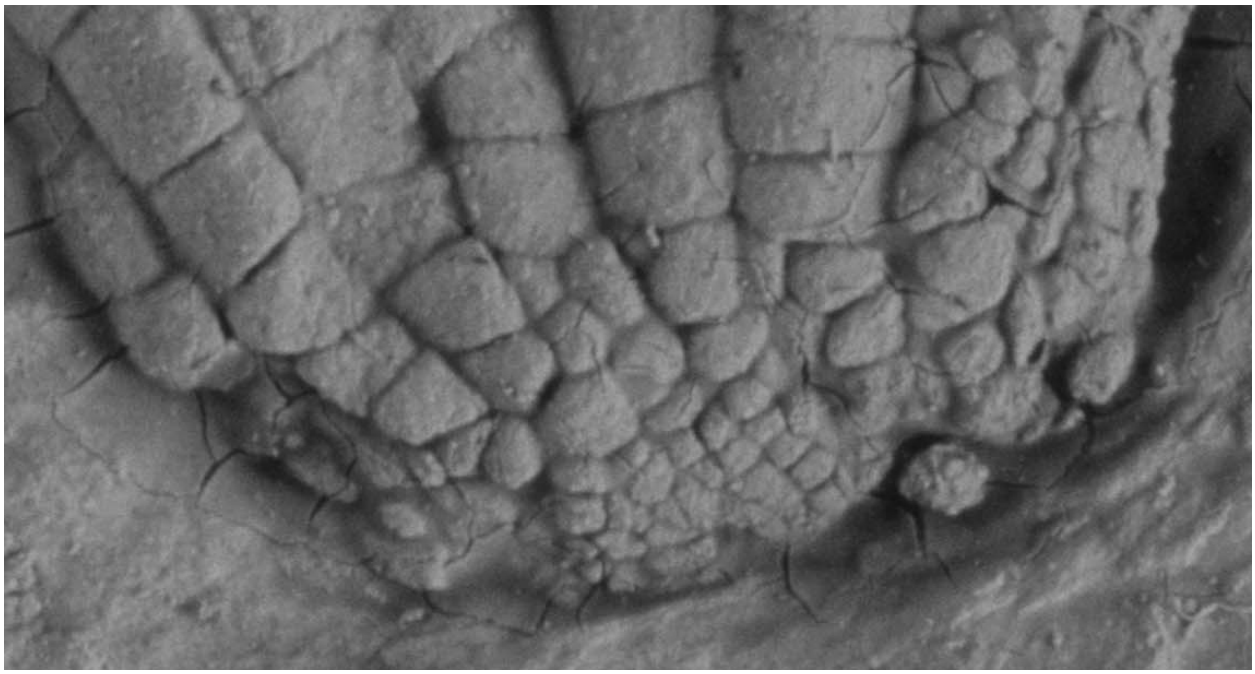


Figure 3.20. Lower pole of a well-preserved specimen, showing attachment pad. Unnumbered specimen from USNM collections; field of view is 6 mm across.

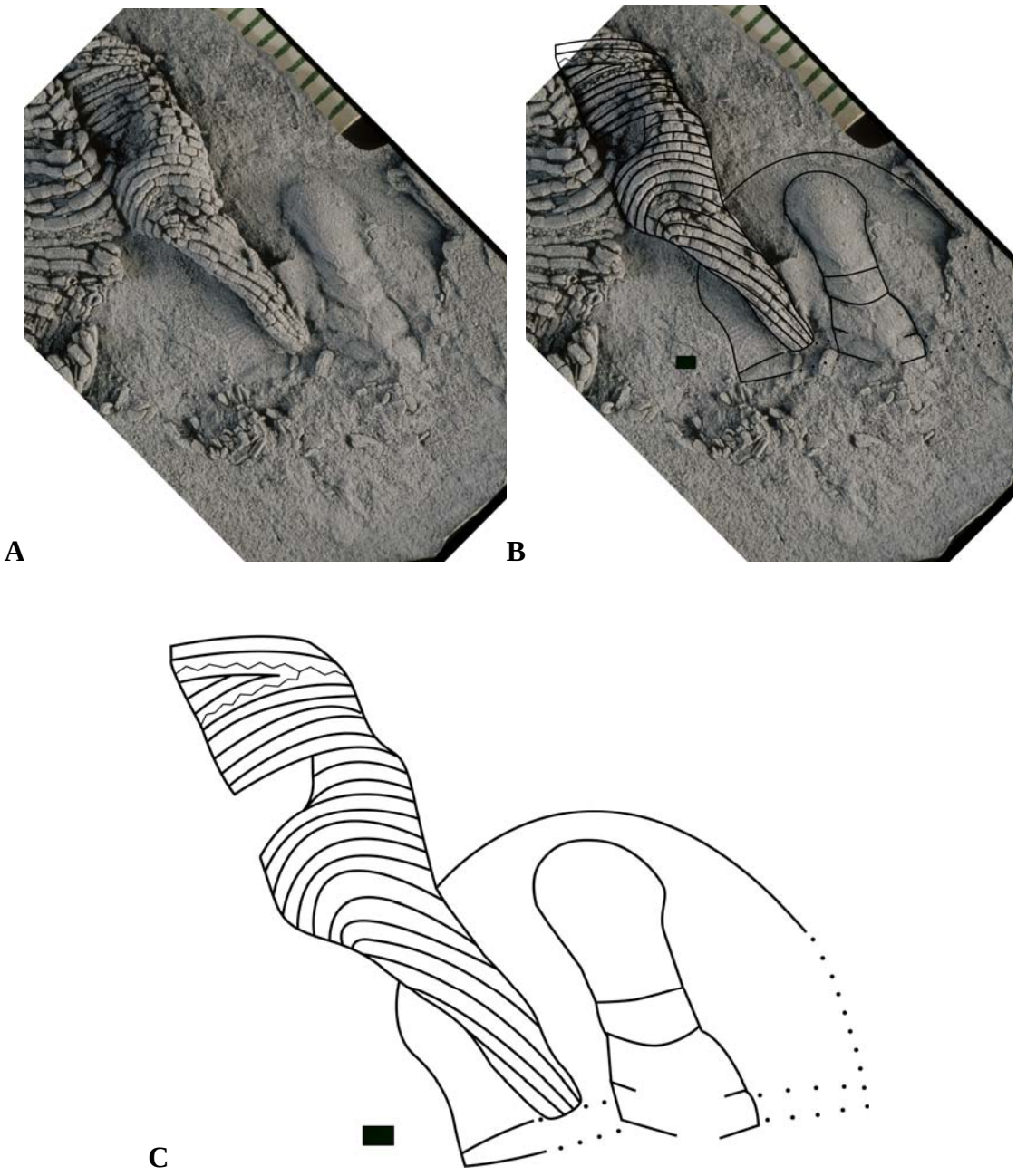


Figure 3.21. Helicoplacoid attached to a *Nevadella* trilobite cephalon. A is an unaltered photograph, B shows the outline of the trilobite and helicoplacoid, C is an interpretive drawing. Scale bar in C is 1 mm across.

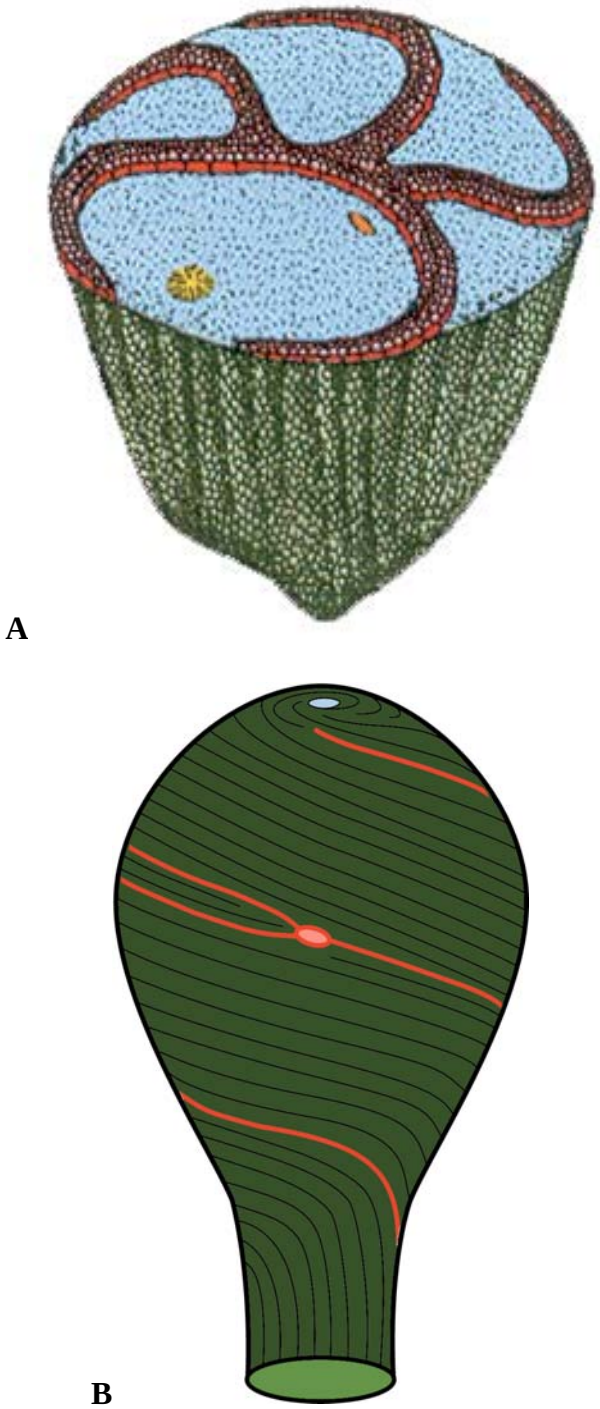


Figure 3.22. Edrioasteroid (A) and helicoplacoid (B) skeletal homologies. Green is the imperforate extraxial region, blue is the perforate extraxial region, and red is the perforate extraxial region. The anus (yellow) and hydropore (orange) of edrioasteroids are small and are likely sequestered in the small disc of perforate extraxial material at the upper pole of helicoplacoids. Figure A is taken from Peterson et al. (2000), which was modified from Paul and Smith (1984).

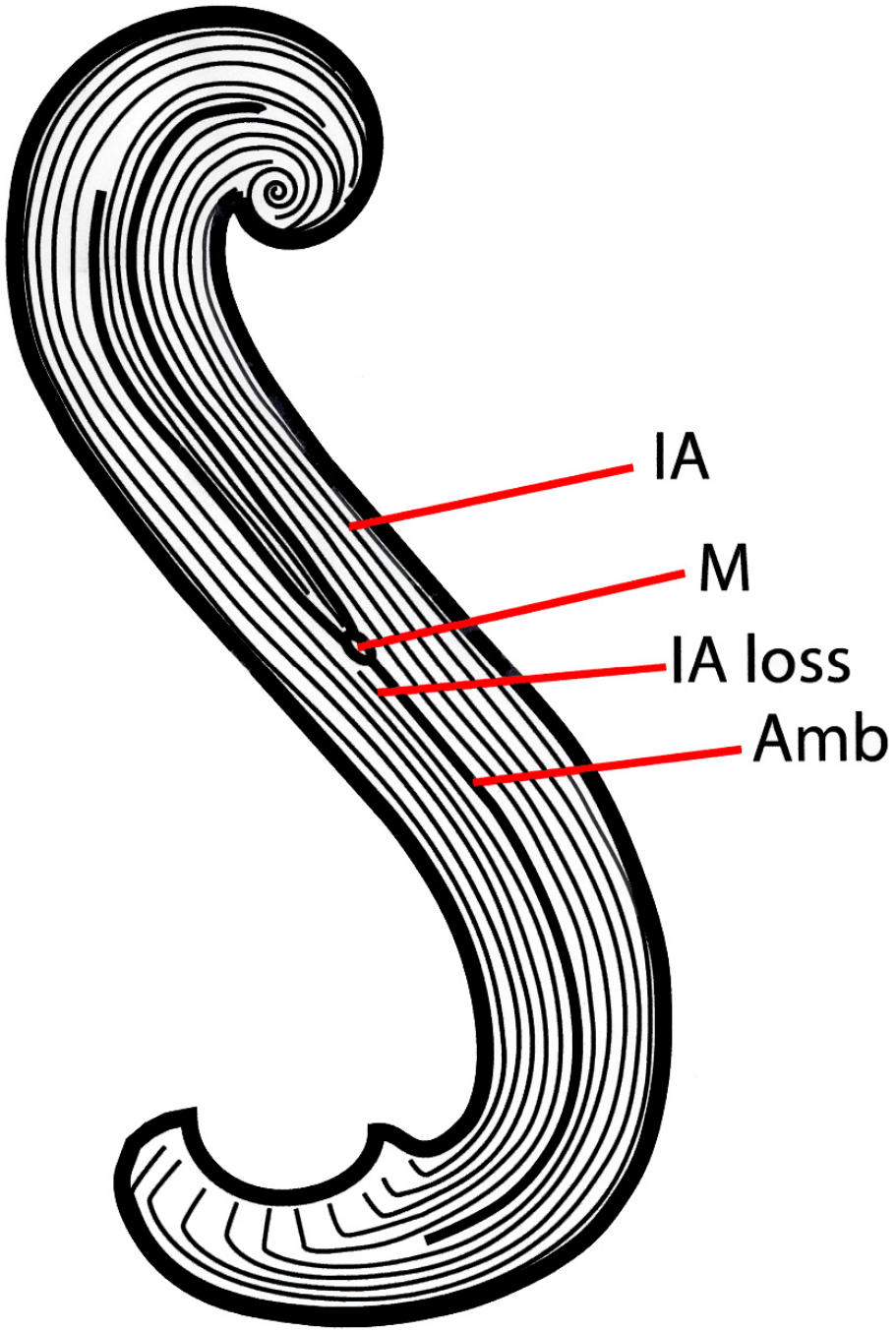


Figure 3.23. Side layout plating diagram of *Helicoplacus gilberti*. IA is the interambulacra, M is the mouth, and Amb is the ambulacrum. Figure modified from Sprinkle and Wilbur (2003, 2005).

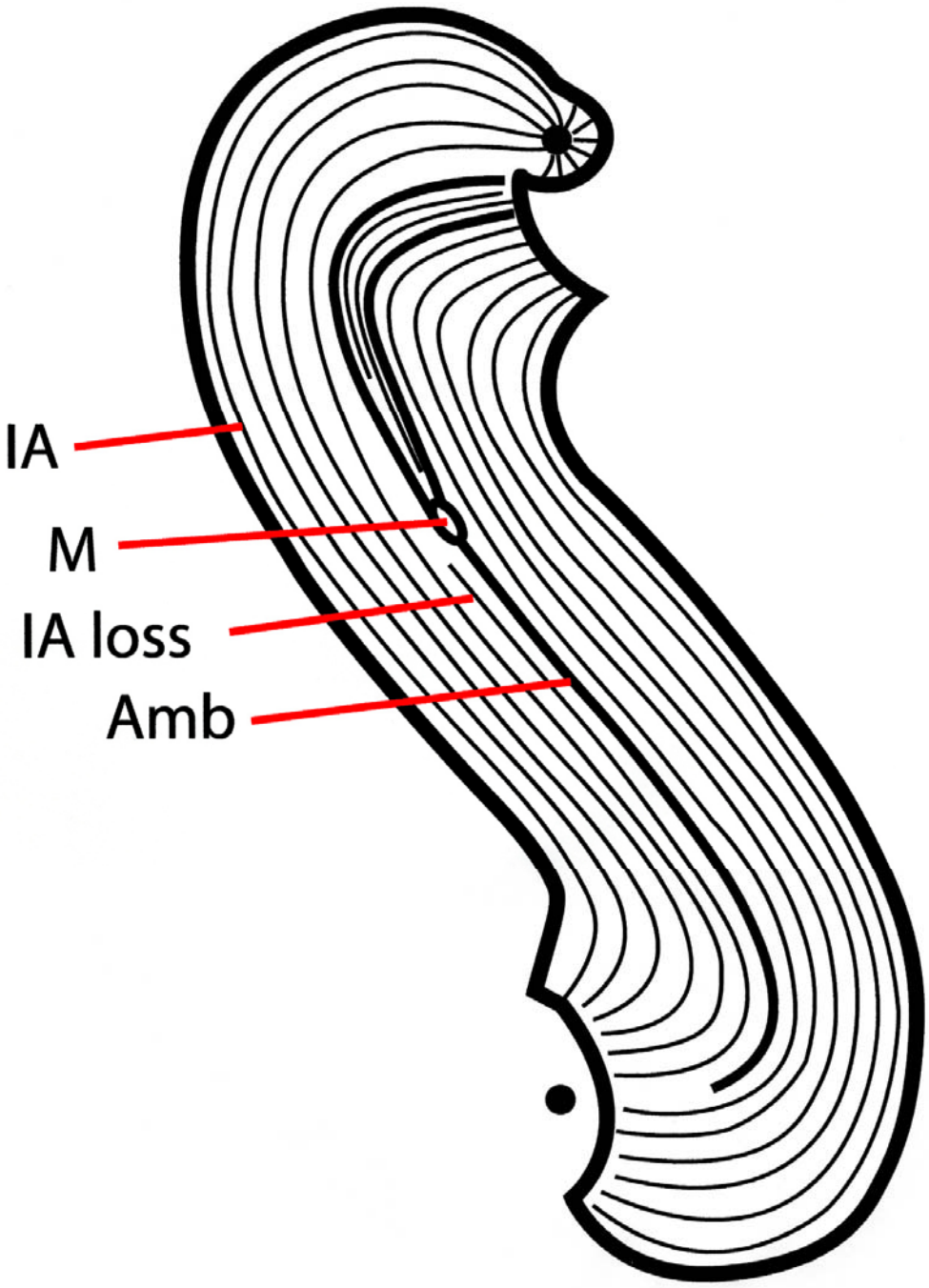


Figure 3.24. Side layout plating diagram of *Waucobella nelsoni*. IA is the interambulacra, M is the mouth, and Amb is the ambulacrum. Figure modified from Sprinkle and Wilbur (2003, 2005).

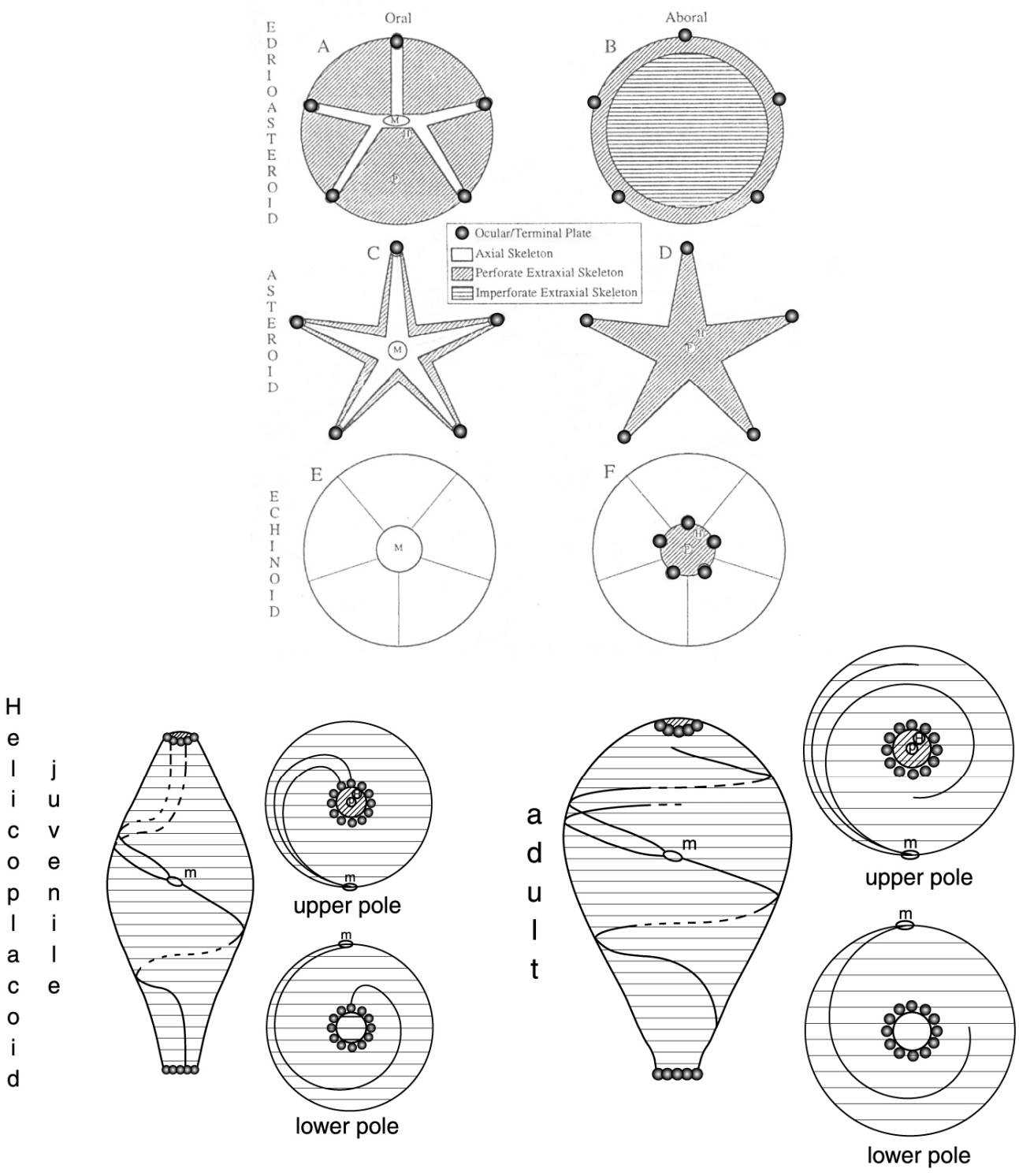


Figure 3.25. Helicoplacoid growth in light of the Extraxial-Axial Theory compared to that of edrioasteroids, asteroids, and echinoids. Note the lack of terminal plates at the terminus of the ambulacra in adult helicoplacoid. The non-helicoplacoid portion of the diagram is modified from Mooi et al. (1998).

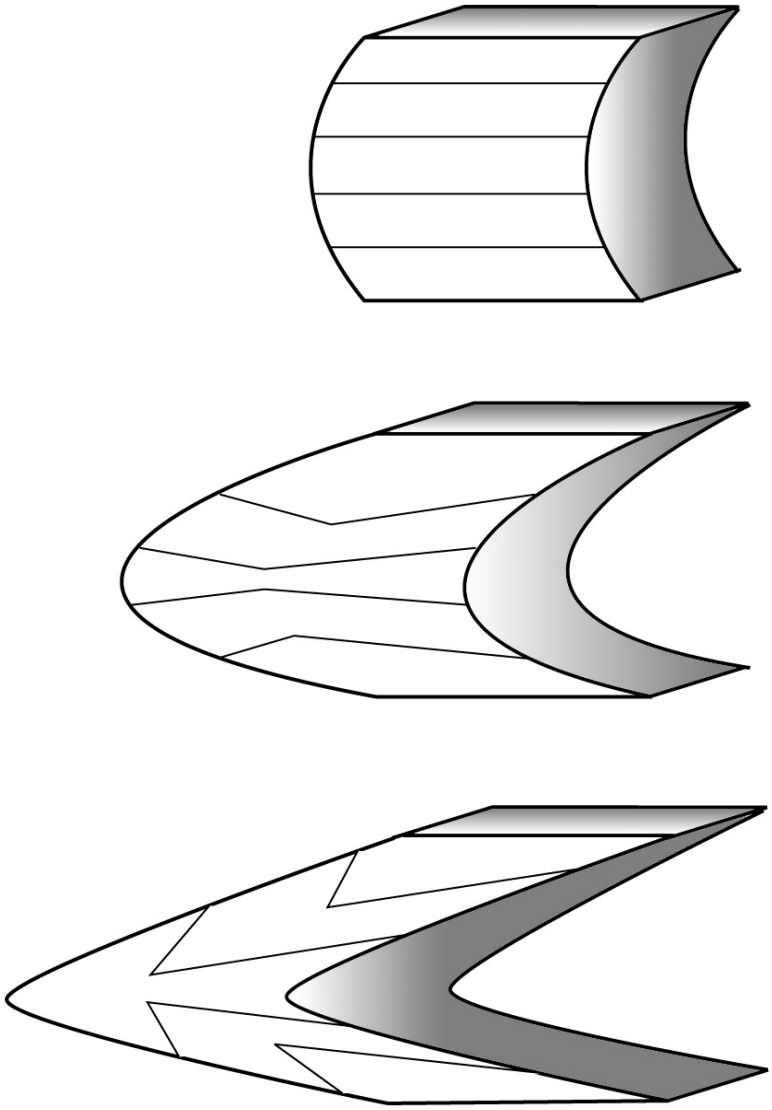


Figure 3.26. Growth series of interambulacral ridge plates. The top position depicts a juvenile-type plate; bottom position is an adult-type plate. Compare to figure 27.

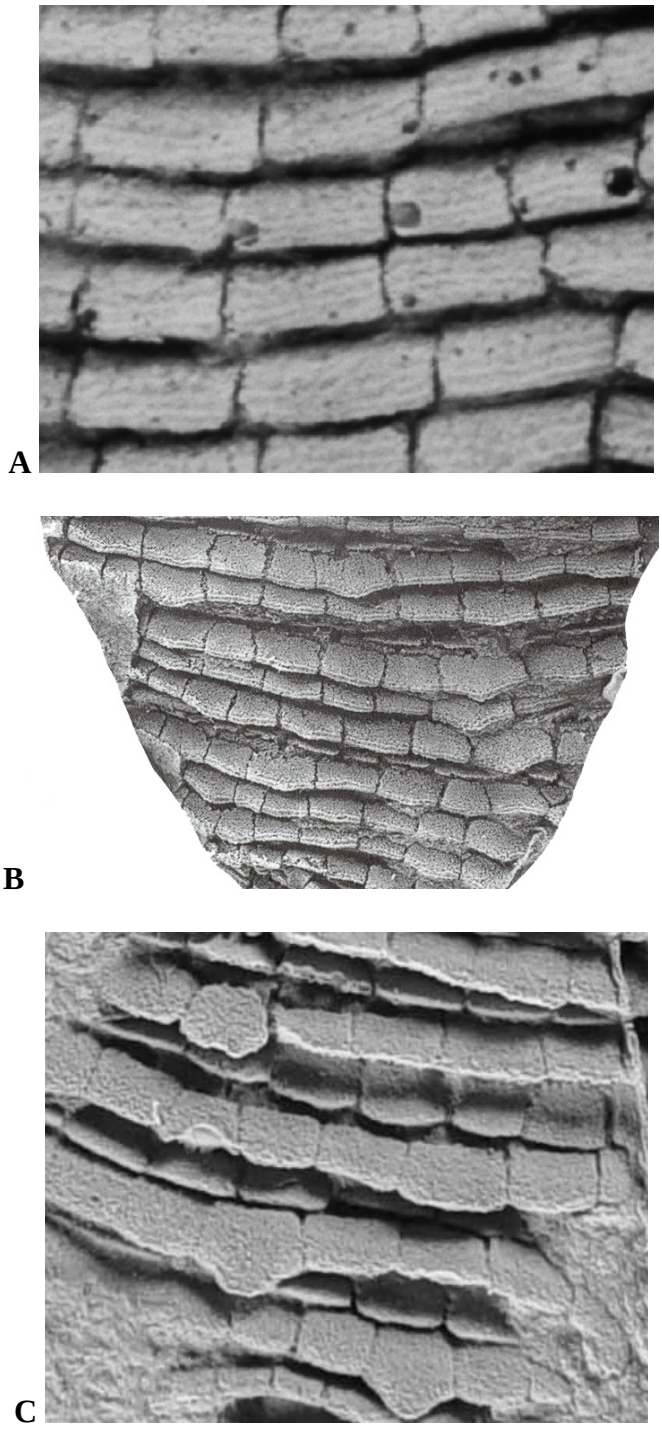


Figure 3.27. Helicoplacoid interambulacral ridge plates arranged in a growth series. A (UCMP 37847) is a juvenile; field of view is 3 mm in height. B (UCMP 14770, from Durham, 1993 [Figure 2-1, pg. 593]) is a middle-aged juvenile specimen; field of view is 10 mm in height. C (UT TMM 2041TX3a) is an adult specimen; field of view is 7 mm in height. Note how plate profile changes the appearance of the plates, especially in B, which shows distortions in the plate ornament.

Figure 3.28. Helicoplacoid in contracted state (UCMP 37847). Metric ruler for scale.

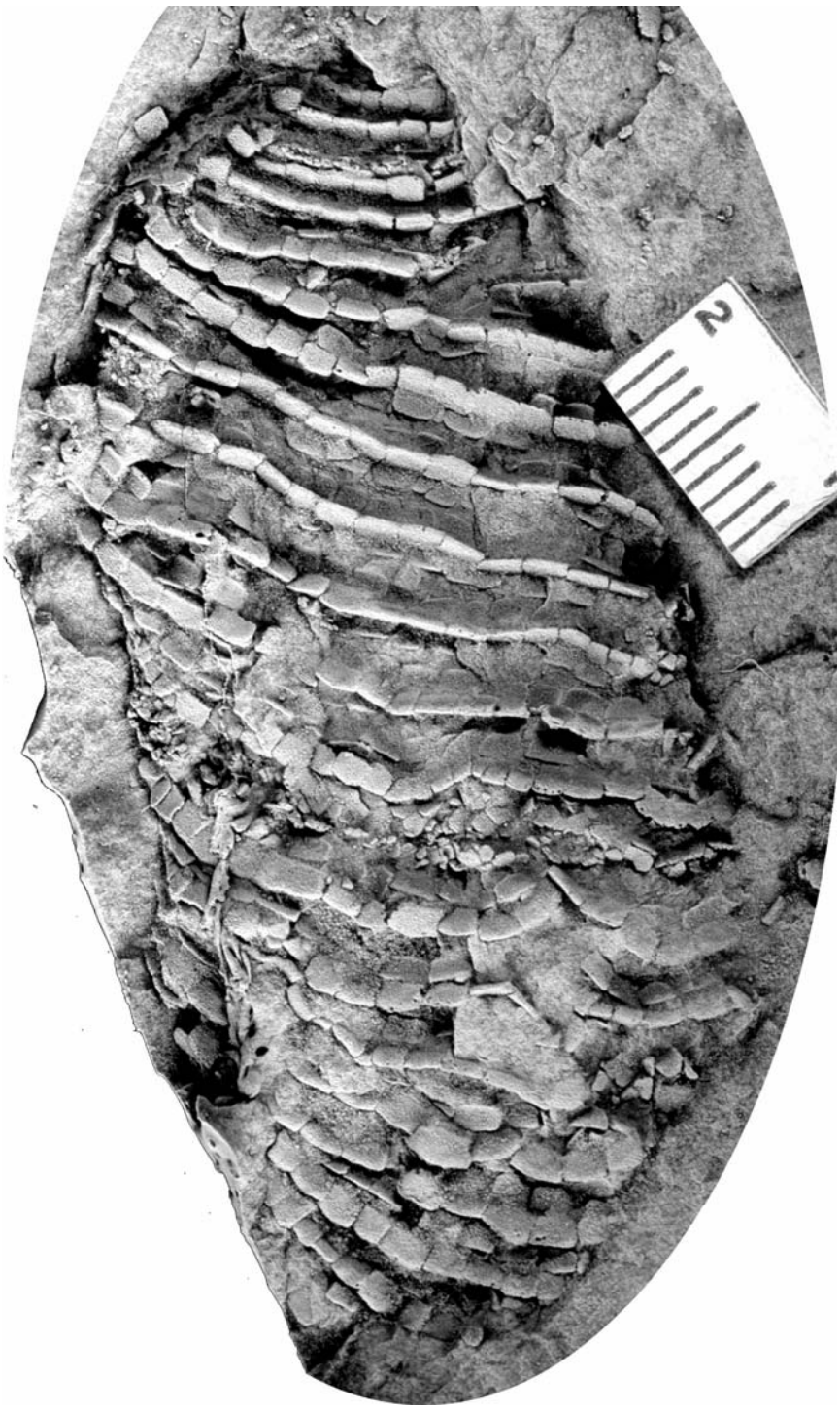


Figure 3.29. Helicoplacoid in expanded state (UT TMM 2032TX2). metric ruler for scale.

Figure 3.30. Helicoplacoid in semi-contracted state (UT TMM 2041TX3a). Note how disparate this and the specimens in figures 28 and 29 appear. These differences were misinterpreted as taxonomic signals by Durham (1993). Metric ruler for scale.

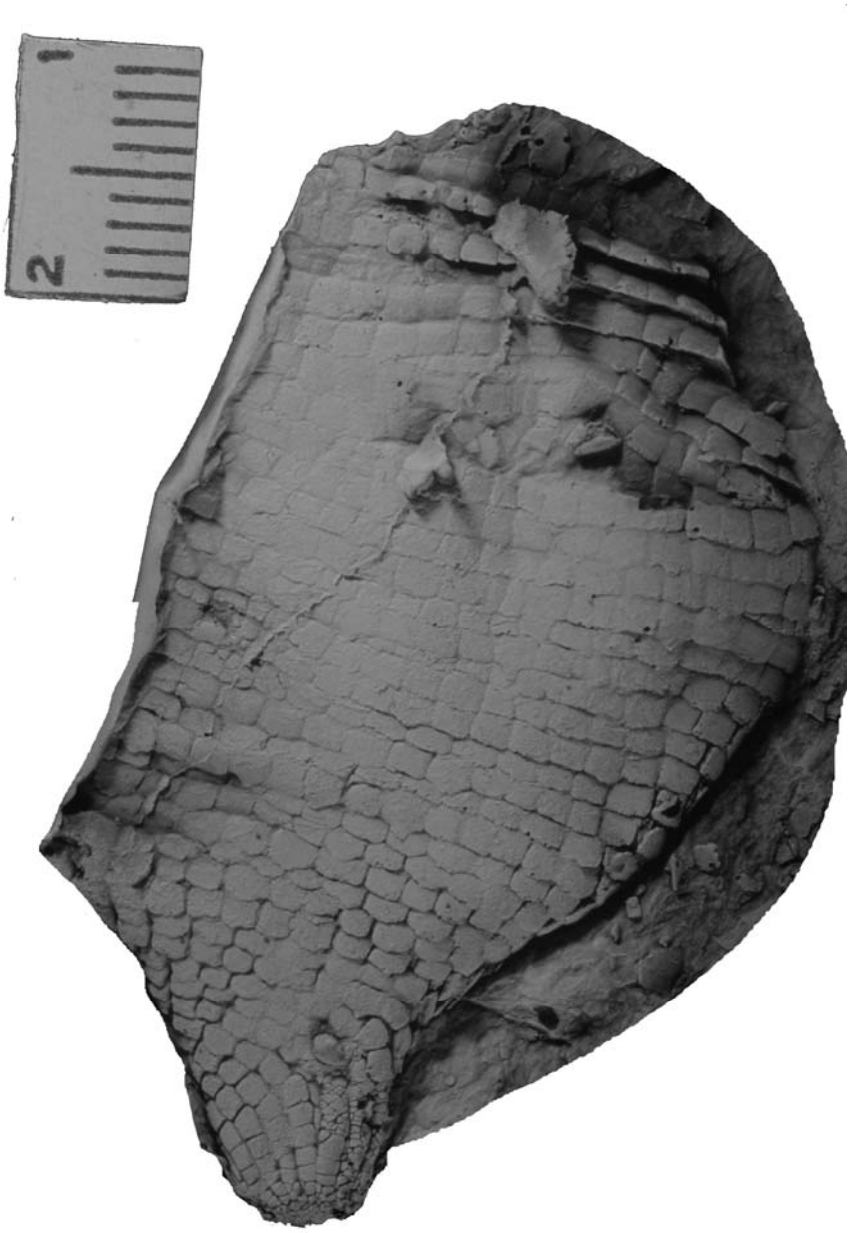
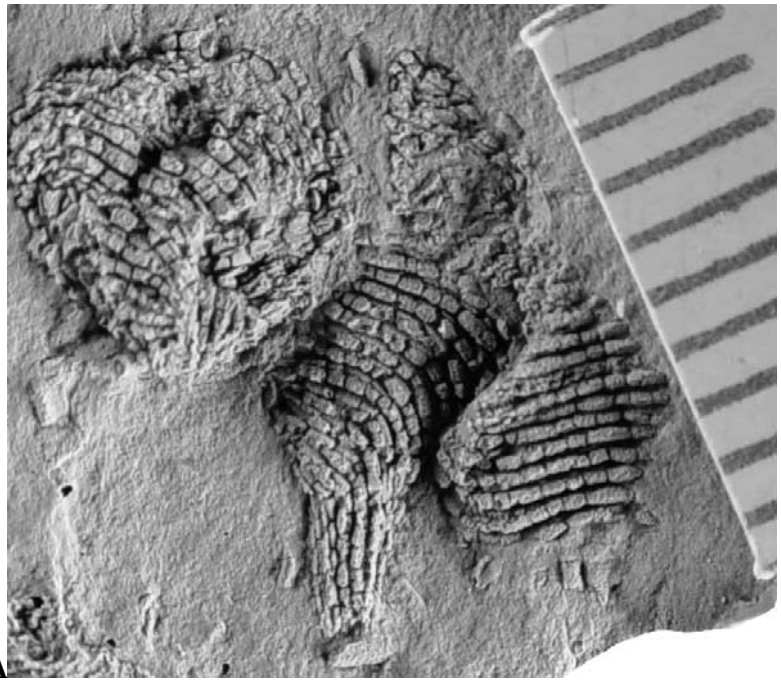
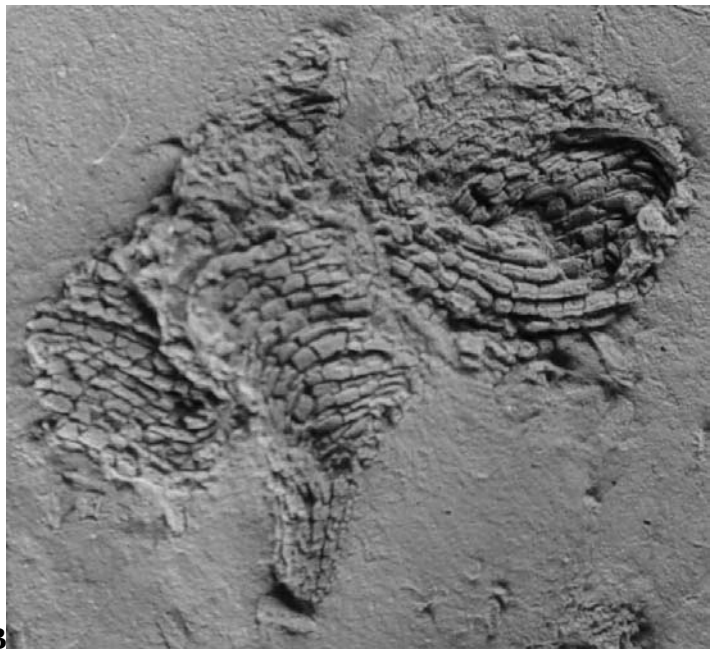


Figure 3.31. Helicoplacoid with downward facing interambulacral ridge plates, forming a pavement. Unnumbered USNM specimen. Metric ruler for scale.



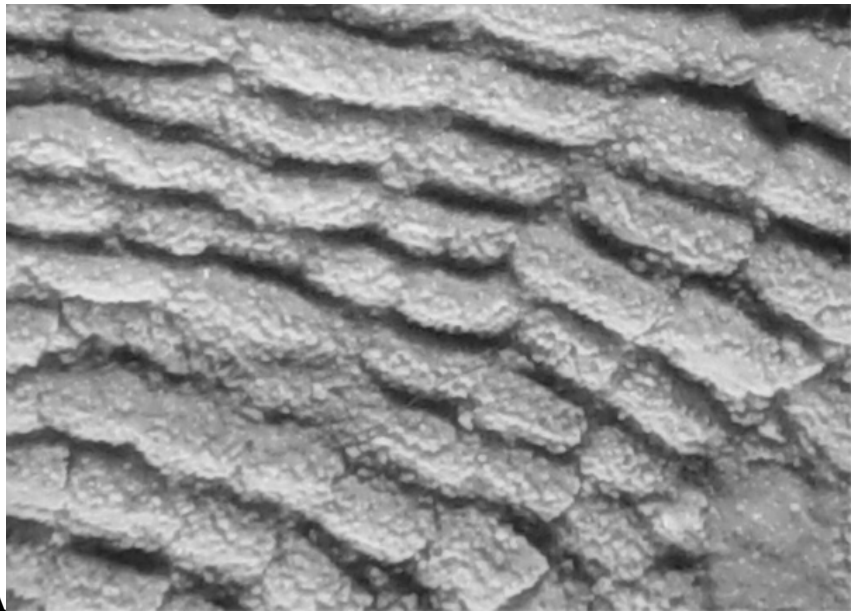
A



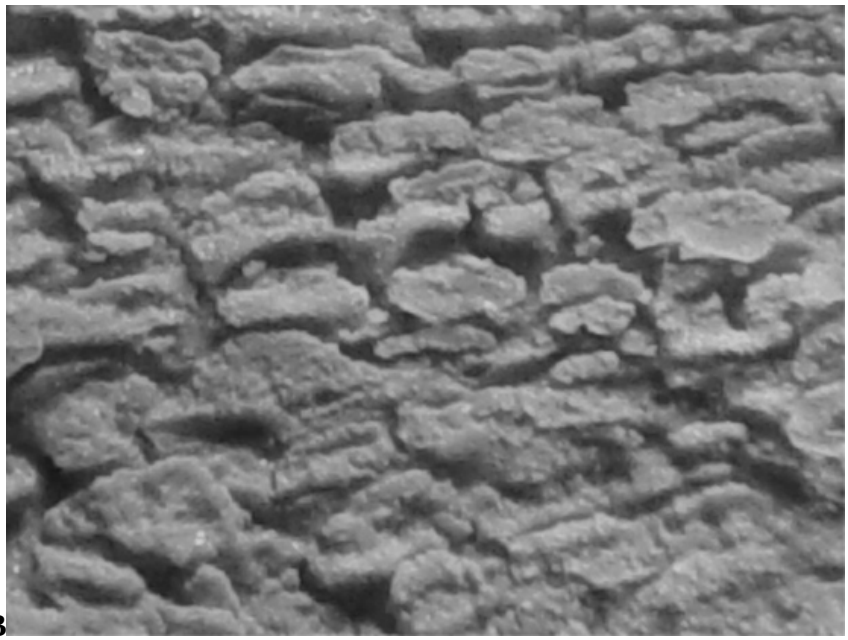
B

Figure 3.32. Juvenile helicoplacoid attached to an isolated interambulacral ridge plate of an adult. A is the part (UT TMM 2041TX4a), and B is the counterpart (UT TMM 2041TX4b). Portion of metric ruler in photo of A for scale.

Figure 3.33. Helicoplacus “sp. b” Durham, 1993. This is a photograph of a specimen collected from the Lower Cambrian *Nevadella* zone, Mural Formation, eastern British Columbia, Canada. The specimen has been assigned GSC 95559, but is currently lost, having been borrowed by Durham for the preparation of his 1993 paper, and not returned before his death. Photograph is from Durham, 1993 (Figure 5-7, pg. 597); specimen is 11 mm tall.



A



B

Figure 3.34. Exterior (A, UCMP 38165) and interior (B, UCMP 38165) of *"Helicoplacus guthi"* Durham, 1993. Pustules are not conspicuous in photograph of interior, but do show near the bottom of the photo. Field of view in A is 8 mm across; field of view in B is 7 mm across.

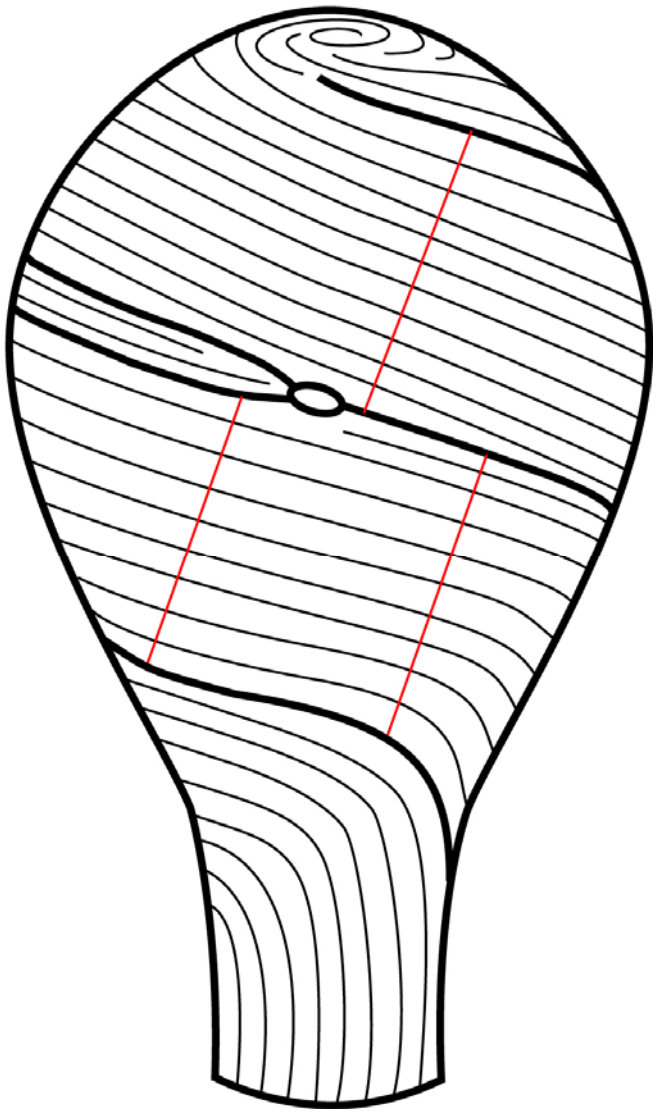


Figure 3.35. Helicoplacoid interambulacral counting. On a complete model, there are 8, 9, or 10 interambulacral ridges between the ambulacrum, depending on where the count is taken. Red lines show three different transects that show three different numbers of interambulacral ridges.

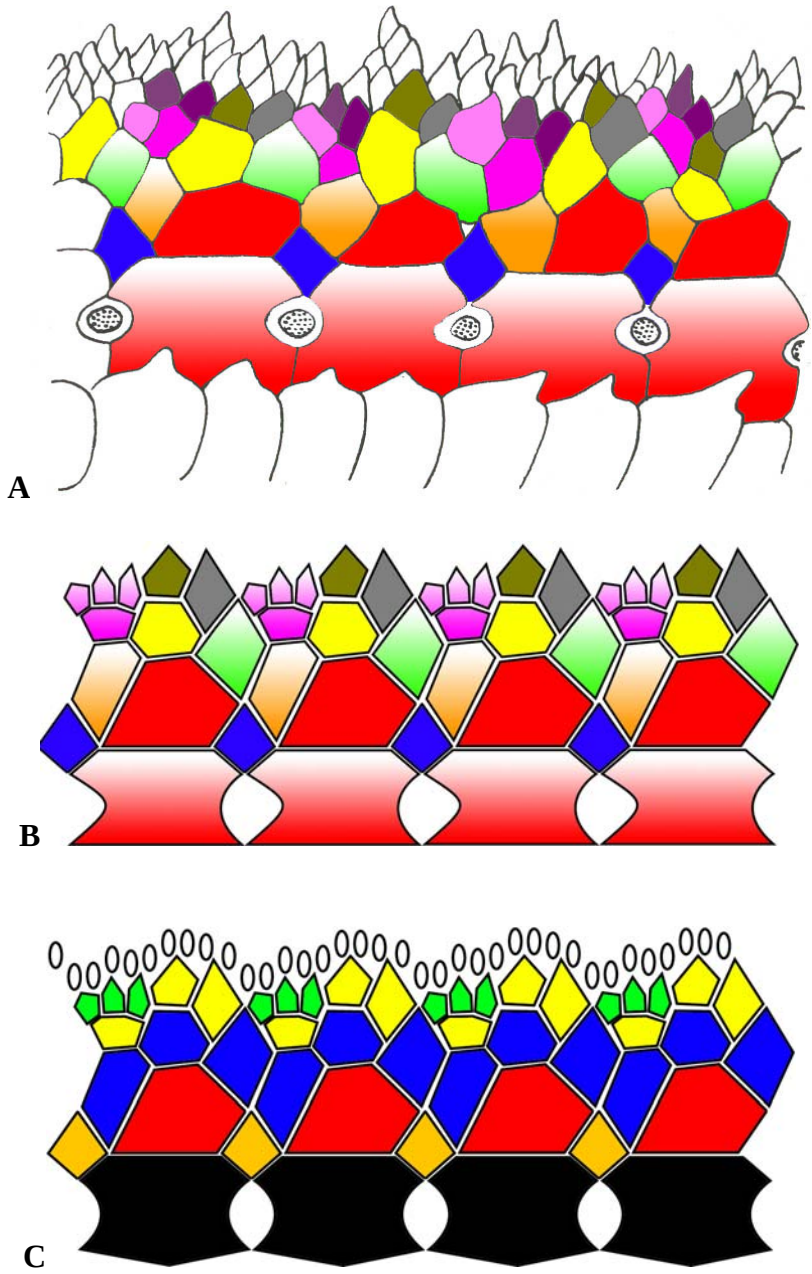


Figure 3.36. Diagram (A) and model (B) of the ambulacra of *Waucobella nelsoni*. Colors in A and B lack meaning; they exist only to show patterns between the diagram and model. C is derived from A and B; black represents floor plates, orange represents rhombus-shaped plates, red represents the primary ambulacral cover plates, blue are secondary, yellow are tertiary, green are quaternary, and white are quintenary. A is an accurate reconstruction modified from Durham (1967, Text-figure 1, pg. 100).

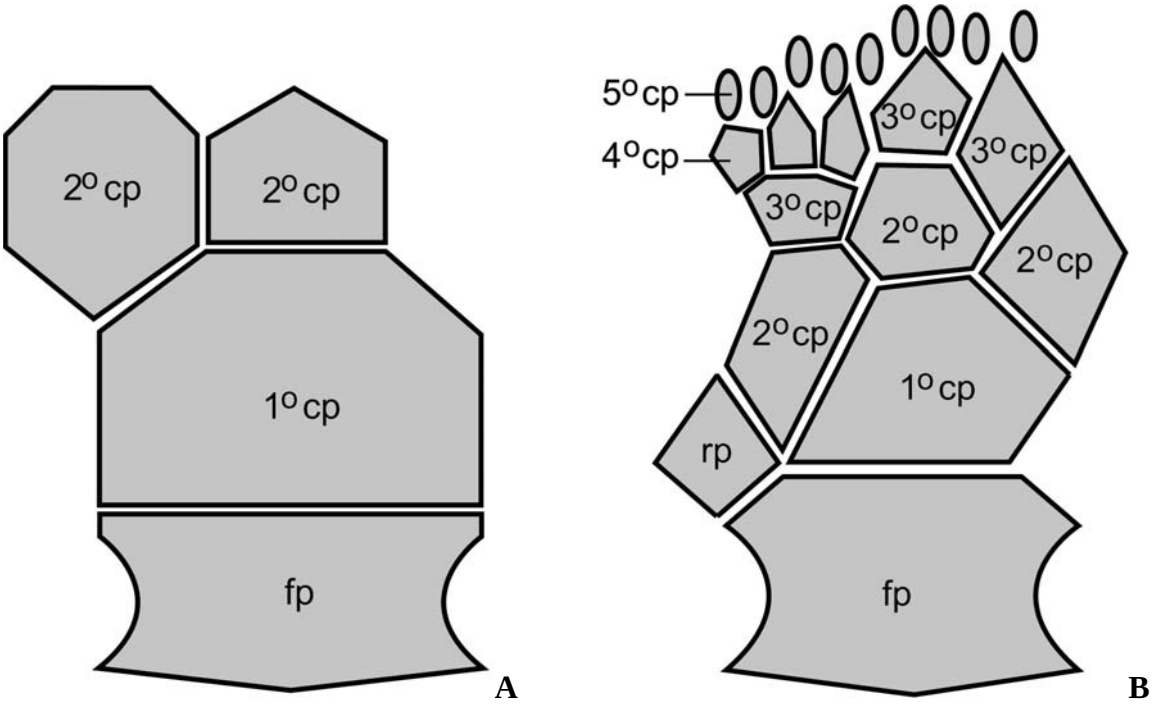


Figure 37. Comparison of the tessellating unit of the ambulacrum of *Helicoplacus gilberti* (A) and *Waucobella nelsoni* (B). 1º cp is the primary coverplate, 2º cp is the secondary coverplate, 3º cp is the tertiary coverplate, 4º cp is the quaternary coverplate, 5º cp is the quintinary coverplate, rp is the rhombus-shaped plate, and fp is the floorplate.

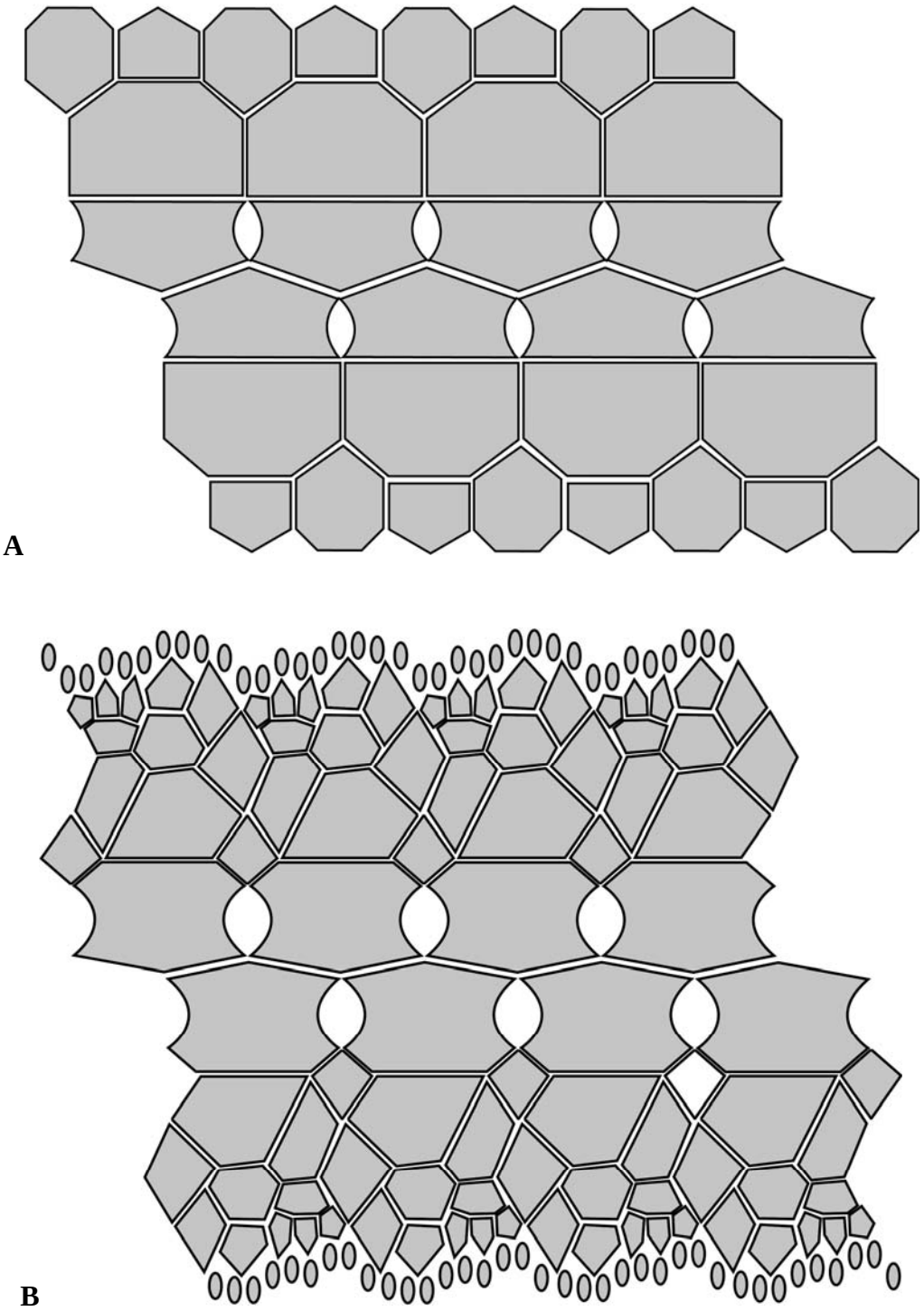


Figure 38. Comparison of complete ambulacra of *Helicoplacus gilberti* (A) and *Waucobella nelsoni* (B). View is from above, with the cover plates retracted, exposing the floor plates. The most useful diagnostic tool is the rhombus-shaped plates found at the junction of the floor plates and cover plates.

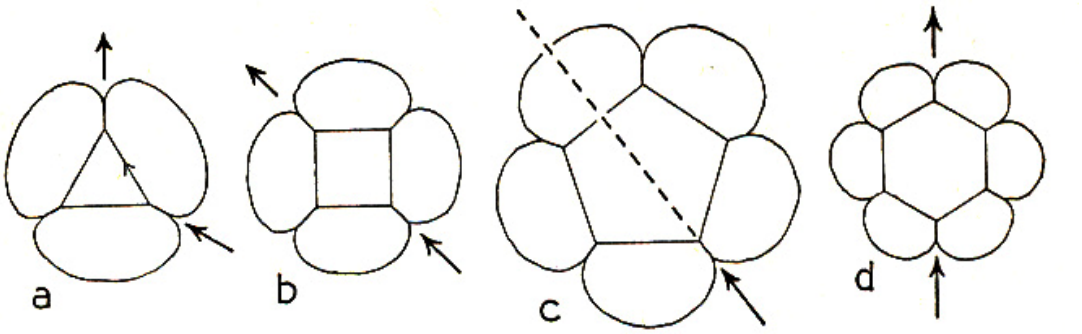


Figure 39. Illustration by Nichols (1969, Figure 20 a-d, pg. 121) showing planes of weakness in a ring of three, four, and six skeletal ossicles, but not in a ring of five.

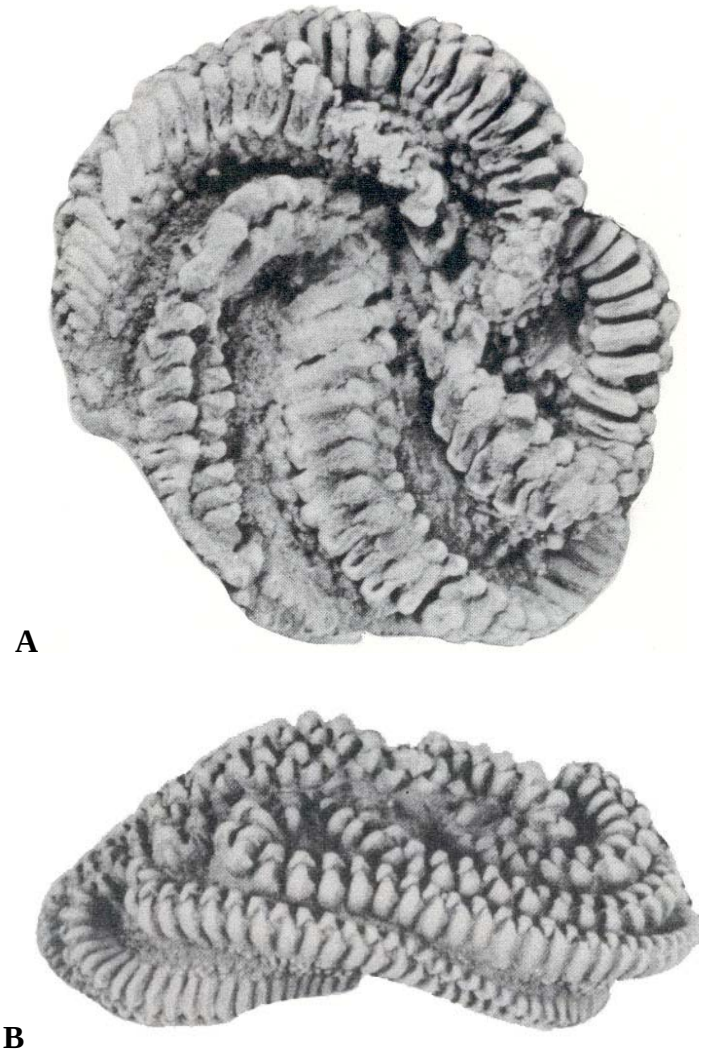


Figure 40. *Streptaster vorticellatus* Hall, 1866. A, from the Museum of Comparative Zoology (MCZ 520), is photographed from above, showing uniformly counterclockwise curved ambulacral tips. B (MCZ 514) shows a side view, indicating upward growth in a left-handed spiral. Photographs are from Bell, 1976 (Figures 9-3 and 9-8, pg. 339); A is approximately 13 mm in width, B is approximately 12 mm in width.

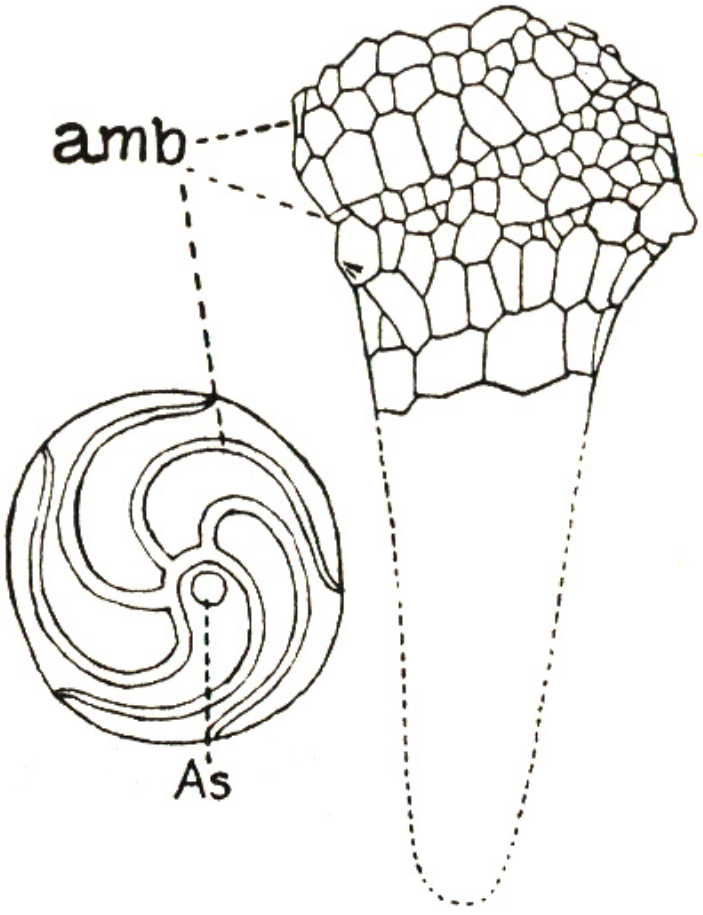


Figure 41. *Gomphocystis tenax* Hall, 1864. Ambulacra curve distally clockwise, twisting the theca into a right-handed spiral. Helicoplacoids are convergent on this body plan, but do so with opposite curvature and spiraling. Specimen is 30 mm in width. Figure taken from Bather, 1900 (Figure 68, pg. 100).

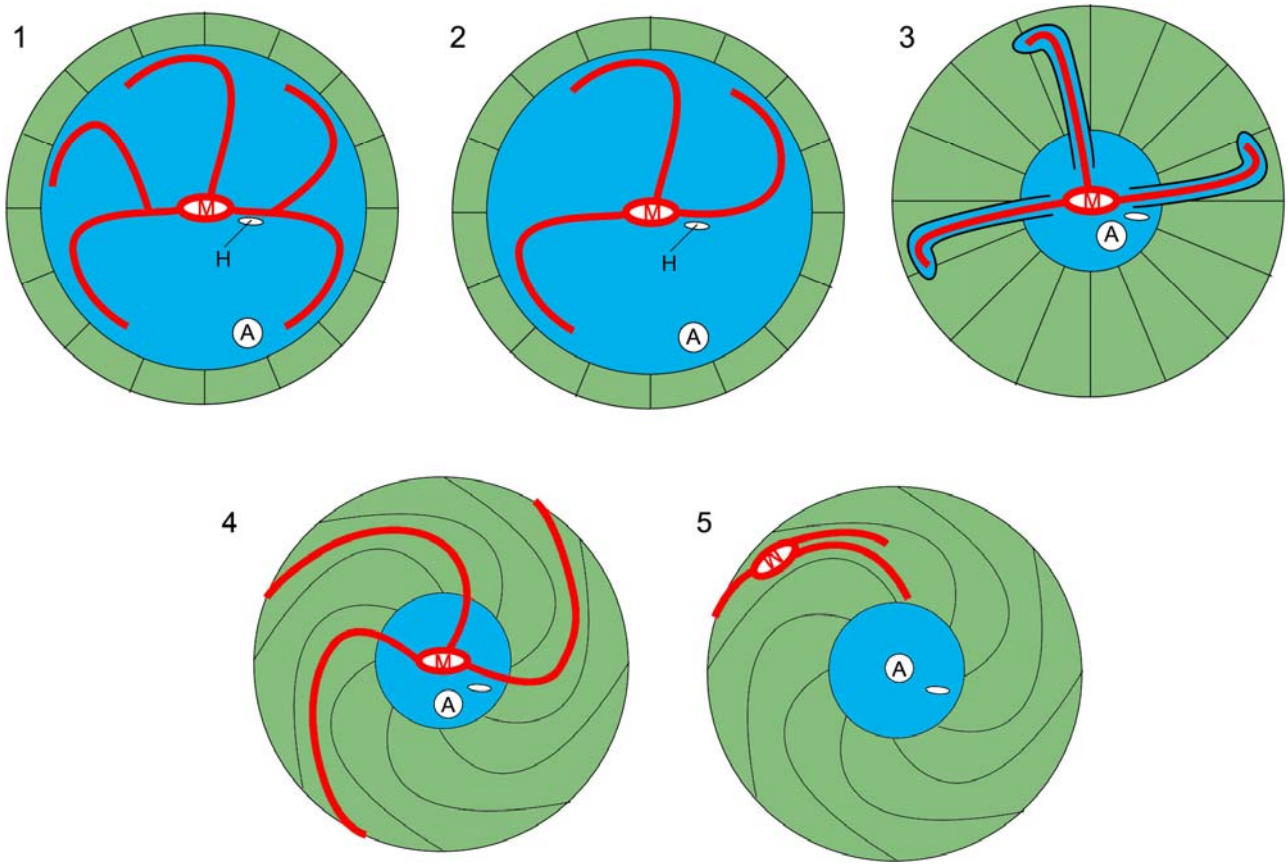


Figure 42. Evolution of the helicoplacoid bauplan from an ancestral pentameral *Camptostroma*-like ancestor, in oral view (1). Ambulacra (red) C and E are lost; C because of the opposite curvature, and E to maintain symmetry (2). The perforate extraxial region (blue) as well as the anus (A) and hydropore (H) become greatly reduced, being displaced by the imperforate extraxial region (green) (3). This step was likely in response to a shift from respiration by epispires to respiration by cloacal pumping. Steps 2 and 3 may have occurred in the opposite order, or concurrently. The theca began growing into a left-handed spiral away from the sediment surface, the left-handedness being directed by the ambulacral curvature (4). Because of the proximity of the anus and mouth brought about by reduction of the perforate extraxial region, the mouth migrated down the length of the A ambulacrum to avoid befouling of the oral area during defecation.

Chapter 4 - *Gogia*

Introduction

Gogia is a small brachiole bearing echinoderm, with a globular to inverted conical shaped theca, a cylindrical holdfast, and multiple brachioles branching from the surface of the summit (Figure 4.1). Holdfasts vary greatly in length among the taxa, but are generally composed of small plates of varying sizes, terminating in a flexible zone of still smaller plates. The theca is composed of adjacent epispire-bearing polygonal plates. The oral surface houses 3 to 5 ambulacra, which have terminal buds from which the brachioles emanate. Brachioles are straight or spiraled, and are composed of biserially arranged brachiolar plates, each of which is covered by 1 to 2 sets of covering plates.

The stratigraphic interval over which *Gogia* ranges is from the Lower Cambrian *Nevadella* zone (herein) through the Middle Cambrian *Bolaspidella* zone (Sprinkle, 1973). Geographically, the North American range of *Gogia* extends from the Proveedora Hills area of Sonora, Mexico to the Mt. Robson area of British Columbia, Canada, along the edge of the Cambrian continent of Laurentia, making it the most geographically and temporally widespread Cambrian genus of echinoderms (Sprinkle, 1973). Recent finds attributed to *Gogia* from the Middle Cambrian of France (Ubaghs, 1987) and the Early Cambrian of Spain (Ubaghs and Vizcaïno, 1990) extend the geographic range of *Gogia* dramatically. The taxon named *Sineocrinus* from the Middle Cambrian Kaili Formation of China (Zhao, 1994; Zhao et al., 1999) is nearly identical to North American eocrinoids, and will probably under closer inspection be reclassified as *Gogia* in coming years. Further occurrences of non-North American echinoderms represented solely by

disarticulated plates may represent further, if less compelling, evidence of the occurrence of *Gogia* from the Early Cambrian.

All initial work on the group was concerned with the plentiful and widespread Middle Cambrian taxa (Walcott, 1886, 1917a, 1917b; Resser, 1939; Kirk, 1945; Harker and Hutchinson, 1953; Robison, 1965; Sprinkle, 1973). Early Cambrian taxa were not hinted at until the discussion of disarticulated echinodermal plates referable to *Gogia* in Sprinkle, 1973. The first complete specimen to be described was *Gogia ojenai* Durham, 1978 of the *Bristolia* subzone of the *Bonnia/Olenellus* zone of eastern California. This single specimen is exceedingly well preserved, but was and still is unique. Following this work was the report of *Gogia* (*Alanisicystis) andalusiae* Ubaghs and Vizcaïno, 1990, a new *Gogia* from the Early Cambrian of Spain. This species is from the Marianian Stage of Spain (Ubaghs and Vizcaïno, 1990), which correlates with the lower *Bonnia/Olenellus* zone (Zhuravlev and Riding, 2001), making the occurrence roughly coeval with that of *Gogia ojenai*. Since then, several new finds have surfaced, all of which follow the trend established by *Gogia ojenai*, in that they are very hard to come by. Most have come to light through extensive collecting by amateur trilobite collectors who have spent many leisure hours logged in the field, and have graciously donated the specimens. Furthermore, all new finds follow a general trend seen in the genus; namely that there exists a single species for each horizon and each locality (Sprinkle, 1973).

Materials and Methods

Gogia and all other echinoderms, built a skeleton out of single crystals of high-magnesium calcium carbonate, which is either preserved intact or replaced, usually by

carbonate. Quite frequently, these carbonate skeletal elements are dissolved away, leaving natural molds of the specimens in the surrounding matrix. The vast majority of all Gogia specimens collected have had their plates dissolved, preserving the fossils as natural molds.

Some minor preparatory work was carried out for a single specimen of *Gogia inyoensis n. sp.*, which had some carbonate skeletal material remaining. This fossil was prepared by repeatedly administering a 10% HCl solution, which slowly etched the plates, then thoroughly rinsed, leaving this specimen as a moldic fossil. Rinsing is requisite to avoid a reaction of residual acid with latex used to cast the specimens.

The natural molds were wetted, then filled with a solution of "Mold Builder" liquid latex rubber, manufactured by Environmental Technology Incorporated of Fields Landing, California, and black powder tempera, manufactured by Palmer Show Card Paint Company of Troy, Michigan. Upon drying, which takes on average three days depending on thickness of latex applied and humidity, the latex is slowly peeled away, resulting in a blackened latex positive of the moldic fossil. These are then "smoked" by applying an ammonium chloride sublimate that whitens the higher relief of the fossils, leaving the crevasses darkened, highlighting contrasts. The ammonium chloride sublimate is applied by the use of a long tube with a spherical cavity on one end and a bulb with a one-way valve. Ammonium chloride is inserted into the spherical cavity and warmed above a burner. Contracting the bulb causes a fine sublimate to waft across the surface of the cast. The ammonium chloride used in this study was manufactured by Matheson, Coleman and Bell, of Northwood Ohio, Los Angeles, California, and East

Rutherford, New Jersey. The end result is a copy of the animal as it appeared in life, which is far more useful for morphological studies than the actual moldic fossils.

This process is for the most part non-destructive. The blackened latex can in some cases leave a stain where it was applied to the rock. The most serious consequence is the possible excavation of overhanging matrix over the fossil, or rock chips. With care, this situation can be avoided by lightly wetting the fossil before removing the latex.

Specimens Studied

The sole museum specimens studied in the preparation of this chapter were UCMP 14526, the holotype of *Gogia* ojenai, and an unnumbered specimen from UCMP field locality number D-4700. This second specimen is a poorly preserved specimen from the Upper Poleta Formation of eastern California, collected in 1971 by Peter Guth, and sent to Berkeley to be studied by J. Wyatt Durham. Numerous specimens from the Carrara formation of the Emigrant Pass area of eastern California and Latham Shale were donated to the University of Texas by Ed Fowler of Palmdale, California, and Carl Locker, of Healdsurgh, California; additional specimens from the Latham Shale of the Providence Mountains, eastern California were donated by Ed Fowler. The author collected specimens from the Emigrant Pass area. Linda and Michael McCollum of eastern Washington University and Spokane, Washington donated two specimens. The first is from the Saline Valley Formation of western Nevada; the second is from the Carrara Formation of the Groom Range of central Nevada.

History

The first description of skeletal material referable to *Gogia* is of single disarticulated epispire-bearing plates belonging to a taxon named *Eocystites primaevus* Billings, 1868 from the Early Cambrian St. John Group, Nova Scotia, Canada (Figure 4.2). The figured plate has a central domed region, and nine radiating spoke-like projections. Complete specimens of this echinoderm have never been found (Dawson, 1868).

This work was followed by the description of a nearly complete specimen with thecal plating similar to the Nova Scotia material, named *Eocystites ?? longidactylus* (Figure 4.3)(Walcott, 1886). Walcott's new specimens were collected from Middle Cambrian rocks near Pioche, and Bennet's Spring, Nevada. Descriptions of the new animals focus on the morphology of the plates, which allowed for diagnosis as *Eocystites*, and the "arms" which branch upward from the summit of the theca. Plate arrangement is described as being without any apparent order, with indentations to allow for pore development when two like plates are placed in opposition. Thecal plates are of four distinct types; smooth and flat, smooth with a central apex, smooth and depressed with minor concentric ribbing, and plates with well-developed concentric ribbing (Walcott, 1886).

The type specimen shows 14 arms surrounding the incomplete summit, with alternating plating (biserial floor plates) forming the lower portion of the arm, and "pinnulae" (cover plates) organized along the tops. No traces of ambulacral pores were found in the arms or summit (Walcott, 1886).

Bather et al. (1900) scrutinized the fossil described by Walcott in preparation of a fossil echinoderm classification scheme. *Eocystites?? longidactylus* was placed in the grade Pelmatozoa, Class Cystidea, Order Amphoridea, Family Eocystidae, which also included *Eocystis* and *Protocystis*, two incomplete forms. As the type specimen of *Eocystites?? longidactylus* is more or less complete relative to the other members of the group, it was taken as the type species of the family. Additions to the body of knowledge regarding this fossil are the identification of stereom in the thecal plating, and recognition that the "pinnulae" described by Walcott along the arms of the specimen were cover plates (Bather et al., 1900).

Twenty years after the publication of the manuscript describing *Eocystites?? longidactylus*, Fred J. Pack, following the 1885 field explorations of Charles Walcott, found several new specimens in rocks from both the Lower and Middle Cambrian, although complete specimens were only found in Middle Cambrian rocks. Pack notes terminological corrections made by Bather (1900) in acknowledging "pinnules" of Walcott (1886) as cover plates, and presence of stereom, but could not identify the latter in the newly collected specimens. This collection did include a specimen with a partial stem, which was heretofore unknown in the group. Straight brachioles are composed of biserial brachiolar plates, with two coverplates per brachiolar plate. Surface characters of brachiolar plates described by Walcott were not found, most likely because previous specimens retained the summit, while this specimen has only the aboral portion. "Lobes" on the plates are placed in apposition to form pores in the theca, with pores disappearing nearer the stem. The incomplete stem is composed of irregularly placed ovate plates of varying size, which allowed for flexibility (Pack, 1906).

Walcott's further tireless exploration of North American Cambrian strata resulted in the discovery of two more early echinoderms, the first of which was diagnosed as *Eocyctites* from the Middle Cambrian Ptarmigan Formation, near Stephen, British Columbia, Canada. The specimen is crushed, with a partial calyx and seven spiraled brachioles preserved. Walcott wrote that the poorly preserved specimen warranted at best a tenuously attributed generic assignment (Walcott, 1917a).

The next echinoderm specimen discussed by Walcott is from the Middle Cambrian Mount Whyte Formation, although Walcott wrote at the time that the formation was Early Cambrian in age. It does indeed occur 304 m (1000 feet) below beds containing organisms referred to by Walcott as *Eocystites?? longidactylus*, but it is found with other Middle Cambrian brachiopods and trilobites. The locality lies above Gog Lake, which lent its name to the genus erected to house this new specimen. Unlike other echinoderms already described by Walcott (1886, 1917a) and Pack (1906) this taxon has a sharply tapered theca with a preserved stem. Epispire-bearing thecal plates are ornamented on the exterior and smooth on the interior, with grooves radiating from the center to edge. Eight long arms are present in the best-preserved specimen, with biserially arranged floor plates, and an "ambulacral furrow" on the interior. The stem is formed from larger rounded or oval plates proximally, and ending at a distal tip with myriad small rounded plates. The specimens figured show long brachioles, and missing plates from the theca, most probably removed during taphonomy. This taxon is sufficiently disparate in gross morphology and the finer details of skeletal plating that Walcott saw it as necessary to place this group in a genus separate from that of

Eocystites, while recognizing that the latter had yet to be found complete. This represents the first mention in print of the name *Gogia* (Walcott, 1917b).

Jaekel considered a new classification scheme for fossil echinoderms, which included a reassessment of the work of and fossils described by Pack and Walcott. According to Robison (1965), the group originally named *Eocystites* was included in the newly erected Order Atava under the family Eocrinidae, subclass Eocrinoidea by Jaekel (1918). Jaekel renamed the specimens described by Walcott with the generic assignment *Eocrinus*, presumably to highlight their inclusion into Class Crinoidea (Jaekel, 1918). Robison (1965) pointed out that despite Jaekel's notation that the name "Eocrinoidea" was first published by him in 1899, that the 1918 paper represents the first published report of the name. Furthermore, the junior synonym *Eocrinus* is invalid, as it post-dates the publication of the valid senior synonyms *Eocystites* and *Gogia*.

C. E. Resser, who worked in the Middle Cambrian Spence Shale of northeastern Utah and southern Idaho, was the next to carry out further work on early eocrinoids. He included figures but no written description of an isolated epispire-bearing plate and the original mold of a nearly complete theca bearing three brachioles (Resser, 1939). The specimen was tentatively identified as *Eocrinus longidactylus* according to the precedent set by Jaekel (1918).

Edwin Kirk in 1945 described a new species of eocrinoid named *Eocrinus multibrachiatus* from the Middle Cambrian Bright Angel Shale of Grand Canyon National Park, Arizona (Sprinkle, 1973). Kirk (1945) recognized the protocol in nomenclature regarding *Eocrinus* as the senior synonym of *Eocystites*, and *Gogia* as senior to *Eocrinus*, but since the new taxon showed more systematic affinities for the

taxon *Eocrinus*, it was placed in that group. The theca is much better preserved in this specimen than in any other North American eocrinoid discovered by that point, allowing for diagnosis of three distinct types of thecal plates. Median plates are large with minor placations (epispires) along the edges, while "proximal" (toward summit) plates are smaller with placations taking the larger part of plate surface area. "Distal" (toward stem) plates are smaller yet, with minor if any placations at all. Thecal plates are loosely sutured. Theca shape is moderately globular as in other specimens of *Eocrinus*, but this group differs from other members of that taxon by having many more brachioles. Kirk (1945) identified twenty, while Sprinkle noticed 24 brachioles attached entirely to one side of the theca, which suggests this group may have had as many as 48 brachioles (Sprinkle, 1973).

The brachioles are long and straight, with what Kirk recognized as a coverplate series ("pinnules" of Walcott 1886). Coverplate sheets could rotate 90 degrees in relation to the flooring plates, which suggested the brachiolar groove, could be closed tight or opened wide (Kirk, 1945).

Harker and Hutchinson (1953) revisited the type locality for *Gogia*, in the Middle Cambrian Mount Whyte Formation in western British Columbia, Canada, on the northern flank of Mount Assiniboine. Walcott considered specimens of *Gogia prolifica* discovered there to be Early Cambrian in age (1917a) because of the Olenellus Fauna at the base of the formation, despite discovering the eocrinoid fossils 131 m (430 feet) above the highest stratigraphic occurrence of *Olenellus*. The newly discovered fossils described by Harker and Hutchinson were found in the *Bathyuriscus – Elrathina* trilobite zone of Middle Cambrian age, which is slightly younger than the Middle Cambrian *Gogia*

discovered by Walcott. These were attributed to the taxon *Gogia prolifica*, primarily because no thecal pores (epispires) were preserved in these specimens, which were taken to be the generic determinant between *Gogia* and *Eocystites*. The calyx was conical and flattened, with smaller plates toward the summit, and larger plates toward the lower theca. Larger plates were recognized as having crenulations along edges, but these were not deemed to be sutural pores. Nine brachioles branch off of the theca, with biserial brachiolar plates and cover plates in a 1:2 ratio. The authors note that this accounts for the first note of preservation of brachiolar cover plates in *Gogia prolifica* (Harker and Hutchinson, 1953).

Robison (1965) added two new species to the taxon *Gogia*. The first, *Gogia spiralis* of the Middle Cambrian Wheeler shale of Utah is diagnosed as having 8 to 12 brachioles in a distinctive left-handed spiral. The conical theca is composed of approximately 100 unornamented plates with sutural pores concentrated near the summit. The hohlwurzel (stem) is complete in these fossils, larger than in other taxa with smaller plates distally, with the whole structure tapering distally, where it is flared. The second, *Gogia granulosa* from the Middle Cambrian Spence Shale is more globular in outline, with eight straight brachioles. The plates that comprise the theca are ornamented with small granules and radiating ridges, with deep sutural pores. The stem is small, with few small plates that get smaller distally, and end in a flattened tip. A final specimen described but not diagnosed in Gogia sp. indeterminate, from the Carrara Formation of eastern California. The specimen includes only the base of the theca and the proximal-most portion of the holdfast, which is significant enough for inclusion in the genus *Gogia*, but insufficient for a specific diagnosis. This specimen is preserved in "The

middle part of the Carrara Formation, near the base of the middle limestone member," rocks that correlate with the *Plagiura-Poliella* trilobite zone (Robison, 1965). This is presumably the Red Pass Limestone of Early Middle Cambrian age (Palmer and Halley, 1979), rather than in the Early Cambrian portion of the formation. Sprinkle (1973) restudied this material and confirmed that this specimen was insufficient for specific diagnosis, but agreed that it did belong in the genus *Gogia*. What remains of the specimen indicates the test is light-bulb shaped, with an elongate holdfast, and straight brachioles (Sprinkle, 1973). This represented the earliest known occurrence of an indisputable *Gogia* at the time of publication (Robison, 1965).

Furthermore, Robison (1965) clarified the synonymy associated with the names *Eocystites* (Dawson, 1868), *Eocrinus* (Jaekel, 1918), and *Gogia* (Walcott, 1917b). *Eocystites?? longidactylus* Walcott, 1886 was placed in *Eocystites* because of an overall plating similarity to temporally and geographically separated isolated plate elements, while the name *Eocrinus* was devised as a senior synonym to *Eocystites* for inclusion into the subclass Eocrinoidea (Jaekel, 1918). The main morphological features delineating these two groups from *Gogia prolifica* Walcott 1917 were an apparent lack of sutural pores and an inverted conical theca in the latter group (Harker and Hutchinson, 1953). After preparation of casts of specimens studied by Walcott (1917b) and Harker and Hutchinson (1953) it was concluded that *Gogia prolifica* indeed had sutural pores upon the theca. Robison reasoned that the thecal shape was not significant enough for maintenance of a separate genus, and subsequently collapsed the three genera into one. The tenuously named *Eocystites* (1868) is a junior synonym to *Eocrinus* (1918), but because publication of the name Gogia predates the publication of the name *Eocrinus*,

and since those specimens attributed to *Eocystites* were subsequently proven to belong to the genus *Gogia,* these groups have been synonymized to the genus *Gogia.*

Therefore, as of Robison 1965, five species represented the genus *Gogia*: *Eocystites longidactylus* Walcott, 1886 was renamed *Gogia longidactylus*; *Eocrinus multibrachiatus* Kirk, 1945 was renamed *Gogia multibrachiatus*; and *Gogia prolifica* Walcott,1917b; *Gogia granulosa* Robison,1965 and *Gogia granulosa* Robison,1965 remained unchanged. All of the named species as of 1965 were Middle Cambrian in age, with mention of an unnamed partial specimen from the Middle Cambrian Carrara Formation, and the isolated plates of *Eocystites* from the Early Cambrian St. John Formation.

Sprinkle (1973) completed the most comprehensive work on the genus *Gogia.* The work of Robison (1965) was built upon and expanded, including the addition of six new taxa to the five discussed by Robison. These include *Gogia hobbsi,* from the Middle Cambrian Cash Creek Quartzite of Idaho, *Gogia kitchneresnsis,* from the Middle Cambrian Stephen Formation, *Gogia palmeri,* from a "Spence Shale Equivalent" of Idaho, *Gogia guntheri,* from the Middle Cambrian Spence Shale, Langston Formation of Utah, *Gogia (?) radiata,* from the Middle Cambrian Burgess Shale Member of the Stephen Formation of British Columbia, Canada, and Gogia sp. 1, from an early Middle Cambrian member of the Carrara Formation eastern California. Notably, the one species that apparently could be found at two localities (Stephen Formation upon Mt. Kitchner, and Mount Whyte Formation, Gog Lake), *Gogia prolifica,* was found to represent two species. The specimens described by Harker and Hutchinson (1953) are disparate enough

to be designated a new species, *Gogia kitchnerensis*. After discovering this taxonomic split, Sprinkle (1973) realized the trend of one species of *Gogia* per locality.

Eocrinoid (?) plates from the Poleta Formation of the White-Inyo Mountains of eastern California were included in the discussion of *Gogia* (Sprinkle, 1973). These disarticulated plates are found in siliciclastic beds in the carbonate-dominated lower member of the Poleta Formation, in rocks correlated with the *Nevadella* faunule of the *Nevadella* zone (Nelson, 1976). Six different types of plates were recognized, at least two of which are a reasonably good match to the thecal plating of other echinoderms, while the others may belong to other echinoderm taxa. A further investigation of newly collected plate material from this locality is included herein.

Sprinkle also included the most comprehensive diagnosis of the genus, of which *Gogia prolifica* Walcott 1917 is designated the type species. Notable synapomorphies for the group are as follows: irregular multiplated globular or barrel-shaped calyx composed of 40-100 plates, a hollow cylindrical irregular plated holdfast for attachment, and three to 45 biserial brachioles radiating from a projections along the edge of the oral surface, employed in the service of food gathering. Brachioles are either straight or spiraled, but never both, with one or two sets or coverplates roofing the brachiolar food groove. Epispires present upon the entire calyx surface or confined to the adoral portions. The mouth is central at the summit of the calyx, with three to five ambulacral areas radiating toward the thickets of brachioles. The anal pyramid is lateral just below the summit (Sprinkle, 1973).

Further isolated Early Cambrian plates similar to the large ornamented epispire-bearing thecal plates of *Gogia* were reported by Mount (1974) from the Chambless Shale

of southeastern California, *Bonnia-Olenellus* zone. A nearly complete specimen surfaced in the underlying Latham Shale, also in the *Bonnia-Olenellus* zone. Mount (1976) diagnosed this specimen as "Gogia new species," and accompanied it with a rudimentary drawing. This same specimen was properly described by Durham (1978), and redescribed herein. The globular theca is 18 mm in diameter, with larger epispire-bearing plates occurring near the summit, and smaller plates lacking epispires near the stem. As few as four epispires are found on the surfaces of small plates, while as many as 18 are found on larger plates. Large plates are ornamented with radiating ridges, and in some cases small pustules. Ten long spiraled brachioles are preserved on this specimen, with coverplates intact, and in some cases opened. Two pairs of coverplates roof a single brachiolar plate. The short holdfast is composed of uniform sized globular plates, and has a large flattened distal end, which is relatively much larger than those found in other *Gogia* specimens.

Durham offered that this Early Cambrian eocrinoid is ancestral to the Middle Cambrian taxon *Gogia granulosa*, with which it shares pustulose plate ornamentation and spiraled brachioles, despite the latter having a less globular theca. The new eocrinoid was named *Gogia ojenai*, and remains the only named member of *Gogia* from the Early Cambrian (Durham, 1973). Durham did however comment on a possible new *Gogia* from the Early Cambrian Poleta Formation mentioned by Sprinkle (1976) as another possible specimen of *Gogia*, discussed herein. Durham noted that it differs from the isolated plate material found in the Lower Poleta Formation (Sprinkle, 1973) in having a different plate ornament, while not ruling out the possibility that this may represent the same species.

Early Cambrian Occurrences of Gogia

The first mention of Early Cambrian occurrences of *Gogia* is of disarticulated epispire-bearing material from the Pioche Shale reported by Pack (1906). Similar material was found at two separate stratigraphic intervals within differing trilobite zones. The lower shale member entombed skeletal plates identified as *Eocystites?? longidactylus*, and the trilobite *Olenellus gilberti*, which is a member of the *Olenellus* zone of late Early Cambrian age (Palmer and Halley, 1979; Mount, 1980). This shale unit is 121 m (400 feet) thick, and is overlain by a 182 m (600 foot) thick limestone unit, which is in turn overlain by a 23 m (75 foot) thick shale unit that contains the remains of *Eocystites?? longidactylus* as well as the trilobites *Bathyuriscus* and *Zacanthoides* (Pack, 1906), which are members of the Middle Cambrian *Bathyuriscus-Elrathina* zone (Lochman-Balk and Wilson, 1958; Sprinkle, 1973). The lower shaly unit correlates with the late Early Cambrian shales of the Carrara Formation (Death Valley Facies) and the Saline Valley Formation (White-Inyo Mountain Facies); the middle limestone unit correlates with the Gold Ace Limestone unit of the Carrara and the Mule Springs Limestone of the White-Inyos, and the upper shale correlates with the early Middle Cambrian Pyramid Shale of the Carrara, and the basal shales of the Monola Formation of the White-Inyos (Stewart, 1970; Palmer and Halley, 1979; Mount 1980). While only disarticulated plates are present in the lower shale and complete specimens were found in the Middle Cambrian shales, this is the first report of *Gogia* occurring in the Early Cambrian. The author did not acknowledge the temporal difference, as the trilobite

biostratigraphy of the Cambrian was not teased out at the time of publication (Pack, 1906).

Two newly described species herein occur within the siltstones and mudstones of the Carrara Formation, Emigrant Pass, Nopah Range, Inyo County, eastern California (Figure 4.4). The first, *Gogia inyoensis* n. sp., is found in association with the trilobite *Olenellus gilberti* at a siliciclastic interval at the top of the Gold Ace Limestone within the *Bonnia-Olenellus* zone. Stratigraphically above the Gold Ace is the Pyramid Shale Member of the Carrara Formation (Palmer and Halley 1979; Ed Fowler, personal communication). These rocks contain the remains of the new species *Gogia lockeri* n. sp. This interval lies within the *Nephrolenellus multinodus* zone of the *Bonnia-Olenellus* zone of the Early Cambrian. The Carrara Formation preserves a mixed siliciclastic-carbonate system, situated along the northern edge of Laurentia during the Early Cambrian. These rocks form part of the "Death Valley Facies," a thick package of predominantly terrigenous marine sediments in the vicinity of southern Inyo County, eastern California (Nelson, 1976).

The Carrara Formation extends to the east into the Groom Range of south-central Nevada (Figure 4.3). Within this section is a nodular limestone unit, which contains the original calcite remains of two specimens of *Gogia*. These are unlike all other specimens in that original plate material persists, rather than being dissolved, leaving moldic impressions in the rock. The specimen was collected by Linda McCollum 40 meters below the Lower-Middle Cambrian Boundary, within the *Olenellus* zone of the Carrara Formation. This formation is named the Combined Metals Member of the Pioche Shale

in other publications, but is still coeval with the Carrara found in Nopah Range of eastern California (Linda McCollum, personal communication).

North of the "Death Valley Facies" and further offshore during the Early Cambrian are the "White-Inyo Facies." The earliest worldwide evidence of skeletized echinoderms is found in the Montenegro Member of the Camptio Formation (Moore, 1976 a, 1976b; Nelson, 1976). These rocks are within the *Nevadia* zone of the *Nevadella* trilobite zone. The echinoderms preserved are single plates with epispires along the edges, which are highly suggestive of *Gogia*, and of the original descriptions of *Eocystites* (Dawson, 1868). As is the case with *Eocystites*, a complete animal has yet to be found.

The fossiliferous carbonate-dominated Lower Poleta Formation overlies the Montenegro Member of the Camptio Formation. While no complete specimens of any echinoderm have been found in this member, bedding surfaces of shaly intervals are covered in echinoderm plates, and some lenses of carbonate rock are composed entirely of echinoderm material. Sprinkle (1973) first recognized these plates, and diagnosed them as belonging to *Gogia*. Despite return trips to the Lower Poleta outcrop in the White-Inyo Mountains by Dr. James Sprinkle and the author, no complete specimens of *Gogia* or any other echinoderm have yet been recovered.

The Lower Poleta Formation also contains the remains of archaeocyaths, and *Nevadella* trilobites. The echinoderm plates are found in a wide array of shapes and sizes, but must appear to be from *Gogia*-like echinoderms. Polygonal epispire bearing plates are found with and without ornamentation, indicating plating from different parts of the theca. An additional plating type appears identical to the oral frame plates of

Totiglobus lloydi (Bell and Sprinkle, 1978), suggesting the additional presence of edrioasteroids (Figure 4.5). The shapes and dimensions of these plates are unequivocal proof of the existence of echinoderms during the deposition of the Lower Poleta, and good evidence that one of these echinoderms were *Gogia*.

Peter Guth and H. Wyatt Durham of the University of California Berkeley collected a single slab, part and counterpart, of three poorly preserved specimens of Gogia in the Upper Poleta Formation in 1971. The rocks are from a limy shale above a limestone marker bed and immediately below quartzite beds (Stewart, 1970; Durham, personal correspondence to James Sprinkle, September 22, 1971; Nelson, 1976). The author visited this locality during the summer of 2002, whereupon a new exceedingly poor specimen was collected, as were Olenellid trilobites, placing these fossils in the *Olenellus*-A zone at the base of the *Bonnia-Olenellus* Trilobite Zone, Upper Poleta Formation. Based on comparison to other sections, this is the earliest unequivocal *Gogia* preserved in part, rather than as isolated plates.

The highest stratigraphic interval of the White-Inyo Facies (Nelson, 1976) containing the remains of *Gogia* is from near the top of the Saline Valley Formation. The fossil was preserved in gray-green shale with minor metamorphic fabric, 50 meters below the upper contact with the overlying Mule Spring Limestone (Linda McCollum, personal communication). These rocks are within the *Bonnia-Olenellus* zone, above the occurrence of *Wanneria* in the Saline Valley Formation, and below the occurrence of *Bristolia* in the overlying Mule Spring Formation (Linda McCollum, personal communication), and correlate with the Eagle Mountain Shale member of the Carrara Formation, and the base of the cratonal Latham Shale (Palmer and Halley, 1979).

Gogia ojenai Durham, 1978, the first Early Cambrian representative of the genus *Gogia* to be described, is preserved as a moldic fossil in the mudstones of the Latham Shale of the Marble Mountains area (Nelson, 1976; Durham, 1978; Palmer and Halley, 1979). These rocks are correlated with the *Bristolia* subzone of the *Bonnia-Olenellus* trilobite zone (Palmer, 1976), and with the Toyonian of the Siberian Platform (Spizharskiy, 1984; Rozhnov, 1992, Zhuravlev and Riding, 2001). The overlying Chambless Limestone, correlative of the Gold Ace member of the Carrara Formation and the Mule Spring Limestone of the White-Inyo Mountains (Stewart, 1970; Palmer and Halley, 1979), is reported to contain the remain of eocrinoids, albeit incomplete specimens (Mount, 1976). These thin sedimentary packages are overly Precambrian crystalline basement rocks, and are therefore considered by Nelson (1976) to be cratonal, as opposed to the thick sequences of deeper water White-Inyo and Death Valley facies. However, Palmer (personal communication) considers these to be slightly off shelf of cratonal facies further to the east.

The Latham Shale also crops out north of the Marble Mountains section in the Providence Mountains, which is now a protected area within the East Mojave National Preserve. Ed Fowler of Lancaster, California, collected the new species described herein and named *Gogia fowleri n. sp.* from these rocks in April of 1994, months before the protected status that made the area off-limits to collecting (Ed Fowler, personal communication). According to the initial geologic report on the area, the Providence Mountains Latham Shale outcrop is 17 m to 23 m thick (55-75 feet). It is composed of a fossiliferous greenish gray platy shale, containing the remains of the trilobites *Paternia prospectensis, Olenellus bristolensis, Paedumias nevadensis, and Paedumias clarki*

(Hazzard, 1954). Since this investigation, *Olenellus bristolensis* has been renamed *Bristolia bristolensis*, and has become the indicator species of the *Bristolia* subzone of the *Olenellus* trilobite zone (Nelson, 1976). This correlates with the Toyonian of the Siberian Platform (Spizharskiy, 1984; Rozhnov, 1992, Zhuravlev and Riding, 2001). Furthermore, *Paedumias* has been synonymized with *Olenellus*. The echinoderm fossils were collected 3 meters below the top of the Latham Shale on the northern flanks of the Providence Mountains, about 1 mile southwest of Summit Springs (Ed Fowler, personal communication; Hazzard, 1954).

While the focus of this work is on the Early Cambrian fauna of North America, the occurrence of material that may be referable to the genus warrants discussion. Echinoderms that may or may not be referable to *Gogia* are found in England, Spain, and Russia. The English material, from the lowermost part of the Botomian (Rozhnov et al., 1992) shows plating similar in outline to that of the Lower Poleta, but differing in ornament, which may place it outside of *Gogia*, if specimens complete enough to warrant a description are discovered (Donovan and Paul, 1982). The Russian occurrence, from the uppermost Atdabanian of Siberia, warranted the description and reconstruction of three fanciful echinoderms altogether unlike any complete echinoderm fossils. The plates used for these reconstructions are very similar in shape and variety to those found in the Early Cambrian Poleta Formation, with which the Russian material is contemporary (Rozhnov et al., 1992).

Paleoecology

All specimens of *Gogia* are found in siltstones or shales within mixed siliciclastic-carbonate systems that existed on what was the northern coast of Laurentia during the Cambrian. The package of sediments that contains all known Early Cambrian Gogia specimens is laterally continuous throughout the Great Basin. *Gogia* is found throughout the section in all trilobite zones save for that of Fallotaspis, but notably only in siliciclastic members.

Sprinkle (1973) described *Gogia spiralis* from the Middle Cambrian Marjum Formation, which had a flared terminus to the holdfast, which was used to attach to skeletal debris. Some specimens were attached to trilobite debris while they were buried. New specimens of *Gogia* from the Early Cambrian have similar holdfast structures, and are therefore assumed to have attached in the same manner to skeletal debris lying on the shallow muddy seafloor. This does not necessarily preclude that *Gogia* was equally capable of attaching to reefs, algal mats, biostromes, or other lithified hardgrounds associated with carbonate rocks. However, the higher wave energy associated with shallow water carbonates does preclude preservation of complete specimens. Skeletal debris has in fact been found in the carbonate-dominated Gold Ace Limestone member of the Carrara Formation, as well as the Chambless Limestone underlying the Latham Shale, and the carbonate dominated ooid shoals and biostromes of the Lower Poleta Formation.

Eocrinoids have brachioles, which are food gathering appendages that branch from the ambulacra, and extend into the water column. The lepidocystids and many Middle Cambrian *Gogia* taxa have straight brachioles, while Early Cambrian *Gogia* taxa have exclusively spiraled brachioles. These are wound into a left-handed spiral in all

taxa save for the case of *Gogia (Alanisicystis) andalusiae*. Several specimens, including *Gogia ojenai*, and *Gogia inyoensis n. sp.* show brachioles upon the same specimen that vary in the wavelength and amplitude of brachiolar coiling. This indicates that brachioles were therefore retractable. A new undescribed *Gogia* from the Middle Cambrian portion of the Carrara Formation of central Nevada shows that straight brachioles were capable of planispiral retraction of the brachioles. Both cases are likely in response to predation.

Sprinkle (1973) considered brachioles to lack an extension of the water vascular system. Ambulacral floor plates are biserial, which is in relation to the biseriality of the biserial branching of the water vascular system, which it supports. As the brachioles also show biseriality, and cover plates, which were likely raised by the action of ampullae (see section on helicoplacoid ambulacra), it is probable that brachioles housed extensions of the water vascular system. Further evidence of these soft tissues is discussed below in the description of *Gogia ojenai*.

Morphology

The Gogia bauplan can be broken down into four major regions which are recognizable in all eocrinoids, and most Early Cambrian echinoderms; the holdfast, theca, oral surface, and the combined ambulacral and brachiolar system.

The Gogia holdfast comprises the basal-most portion of the body. This region varies greatly in size relative to the theca and shape throughout the genus, but in all specimens it is a distally tapering structure composed of relatively smaller unornamented ovoid plates of varying size, terminating at a point composed of smaller plates still. It is this termination, which served as the point of attachment to a substrate, most likely

skeletal fragments (Sprinkle, 1973). The region lacks epispires or any other connection to the interior of the animal. The holdfast terminates in a distal pad, which is morphologically differentiated from the remainder of the holdfast.

The ratio of holdfast length to calyx length varies from as small as 0.3 in some specimens of *Gogia granulosa*, to as much as 2.0 in the case of *Gogia longidactylus*. Holdfast shape varies from narrow and cylindrical in the case of *Gogia palmeri*, to an inverted cone. The single previously described Early Cambrian specimen, *Gogia ojenai* has a holdfast that is flared at the terminus to provide a broad attachment surface, similar to a ring-like termination found in some specimens of *Gogia spiralis* and *Gogia granulosa* (Sprinkle, 1973). It is possible that this type of termination is more common, but the terminus of the holdfast is infrequently preserved.

The theca is composed of plating of both the imperforate extraxial region and perforate extraxial region. A drastic enlargement of plating demarcates the boundary between these two regions, along with the appearance of pores in the theca in the form of epispires. These are notches in the edges of otherwise convex polygonal plates that adjoin the epispires of adjacent plates to form pores. A raised rim makes these structures more conspicuous. Plates are either smooth as is the case of several specimens of *Gogia* included herein from the Carrara Formation, or pustulose, as is the case for *Gogia ojenai*.

The size of the epispires increases nearer the summit. The development of epispires varies from species to species, but generally larger species and larger ontogenetic stages exhibit more developed epispires, as would be expected from problems associated with the ratio of volume to surface area. *Gogia longidactylus* for example has epispires limited to the upper quarter of the theca, while *Gogia granulosa*

has in many cases epispire-bearing plates extending the full length of the theca. Generally, plating is similar to that found upon *Gogia lockeri n. sp.* with epispire plates confined to the upper half of the theca.

The oral surface is situated at the summit of the theca. Epispire-bearing plates form a pavement in the interray between ambulacra, allowing for gas exchange. Unfortunately, the oral surface is poorly known in described specimens, as the theca is usually crushed or disarticulated to the point that the organization is unrecognizable. Generally oral plates are smaller than thecal plates, and have much deeper epispires.

Ambulacral areas are also poorly known in described specimens due to crushing, the small size of the plates, and degradation of the soft tissues holding these plates together. New undescribed specimens from the Middle Cambrian Spence Shale of northern Utah exhibit the 2-1-2 ambulacral area arrangement typical of early echinoderms, so it can be assumed that the Early Cambrian representatives had a similar arrangement. The ambulacral areas are roofed by a biserial coverplate series, which terminate in thickets of brachioles.

Brachioles are food-gathering appendages unique to the blastozoan echinoderms, including lepidocystids and blastoids. The brachioles are either straight or spiraled in a left-hand fashion across the genus, but are exclusively spiraled in Early Cambrian taxa. These structures are considered to have differed fundamentally from the arms of crinozoans by the exclusion of the water-vascular system. Instead, they are hypothesized to have functioned through ciliary action or through employment of a mucous net (Sprinkle, 1973). Here, they are reinterpreted as having extensions of the water vascular system, which is the reason for biseriality. Each is composed of a biserial series of

brachiolar plates, and covered by a series of interlocking coverplates. Coverplate to floorplate ratios range from 1:1 to 2:1. Brachioles vary in number, but generally correlate with size and ontogeny of each individual specimen. However, *Gogia multibrachiatus* has many more brachioles than other species, estimated to have as many as 40 (Kirk, 1945), although Robison (1965) later reduced this to an estimated 22 brachioles. A new specimen of *Gogia lockeri n. sp.* from the Carrara Formation has the most brachioles of Early Cambrian specimens at 16 brachioles.

These body regions are roughly equivalent to readily recognized echinodermal body regions outlined in the Extraxial-Axial Theory (Mooi et. al, 1994, Mooi and David, 1997, 1998). The Imperforate Extraxial Region as defined by David et al. (2000) is the portion of the body wall lacking any orifices whatsoever. This region generally comprises stems and holdfasts in stalked forms, and the aboral surfaces of edrioasteroids. In modern groups the imperforate extraxial region has become lost in all taxa excepting crinoids, in which it is greatly reduced (Mooi and David, 1998). In *Gogia*, the imperforate extraxial region comprises the entirety of the holdfast, but contrary to prior claims, in some groups it also extends summit-ward and composes the basal-most portion of the theca. Small multi-sized plates bearing an angulation grade into larger polygonal plates, which bear an the diagnostic angulation. The placement upon the theca of the boundary between the imperforate and perforate extraxial regions varies within the genus; *Gogia granulosa* has this boundary at the base of the theca, the new species *Gogia fowleri* has this boundary midway between the holdfast and the summit, while in *Gogia longidactylus* this boundary exists nearly at the summit (Sprinkle, 1973). The boundary is marked by a loss of epispires.

The imperforate extraxial region is differentiated into two regions consistent with bodily divisions seen in other Early Cambrian echinoderms; the lower attachment pad constitutes a separate region. The edge of the pad marks the boundary with the flanking region, which makes up the stalk. Stalk plates are inserted here, which grow larger as the animal matures. This is contrary to the assertions of Guensburg and Sprinkle (2001), who asserted that plate insertion occurred at the boundary with the theca. The pattern of smaller plates toward the tip and larger toward the theca are consistent with the interpretation presented here (Figure 4.6).

While evidence exists that the boundary between the imperforate extraxial and perforate extraxial regions varies within the genus *Gogia*, some evidence may be skewed relative to paleoenvironment and ontogeny. Animals found in deeper oxygen restricted environments would be expected to have a greater surface area dedicated to epispire coverage and therefore respiratory capacity. As well, adults have more epispires than juveniles as a smaller surface area to volume ratio necessitates a greater area dedicated to gas exchange.

The perforate extraxial region extends from the upper reaches of the imperforate extraxial region to the summit of the theca, and into the interrays (interambulacral areas), comprising portions of the theca and the oral surface. As already noted, epispires get relatively larger toward the summit. The boundary between the perforate extraxial region and the axial region is found along the edges of the ambulacral areas, with the zone of growth for each at the ambulacral tip. Growth in this region is relegated by the octet rule, as the ambulacral areas grow biserially in order to accommodate the radial water vessels, which have alternating branches that form ampullae and tube feet. Whereas Sprinkle

(1973) argued that the water vascular system did extend into the ambulacral areas, it did not extend into the brachioles. It is argued here that the biserial arrangement of axial skeletal elements is tied to the alternating arrangement of tube feet within the water vascular system. As brachioles are derived from the ambulacral system with the same biserial design, it follows that the underlying cause for biseriality in the ambulacrum is the same underlying cause for biseriality in the brachioles, namely the extension of the water vascular system.

The arrangement of the perforate extraxial region, imperforate extraxial region, and axial system in *Gogia* is similar to the arrangement in other Early Cambrian echinoderms. The aboral pad of *Camptostroma*, the lepidocystids, and the attachment pad of the helicoplacoids are homologous to the pad at the tip of the *Gogia* holdfast. The stalk is homologous to the pleated aboral skirt of *Camptostroma*, the interambulacra of helicoplacoids, and the imbricate theca-enclosing portion of the lepidocystid theca. The perforate extraxial region however is more extensive in *Gogia*, extending beyond the summit and enclosing the upper portion of the theca.

Systematic Descriptions:

This study includes the descriptions of four new species of *Gogia*, two additional new taxa represented by material not complete enough to warrant a description and a name, as well as two occurrence of an echinoderm that is likely *Gogia* from the Early Cambrian succession of the White-Inyo Mountains of eastern California. A discussion of these first two occurrences, represented entirely by single disarticulated plate elements, precedes the systematic descriptions of whole animals.

Montenegro Member Plates

The first worldwide occurrence of unequivocal echinoderms, albeit incomplete specimens, is from the Montenegro Member of the Campito Formation, White Inyo Mountains, Inyo County, eastern California (Nelson, 1962; Moore 1976). Individual pyritized echinoderm plates are preserved in siltstones (Figure 4.7). One such plate is from the upper portion of the theca of an eocrinoid. The plate has a maximum width of 3 mm. The edges are incised by nine deep epispires, suggesting the proposed thecal position. The deepest epispire is approximately 1 mm in length, the shortest a fraction of that. The plate is preserved as a part-counterpart pair. Relief on both the positive and negative indicate the plate was convex outward, with the high relief of the center of the plate extending to the edge of the plate in radiating ridges, each of which is edged by an epispire.

A second plate from the same formation also shows the diagnostic invagination of epispires. The plate has a length of 4 mm, and a width of 3 mm, and is filled with small pyrite crystals on both the part and counterpart. The border of the plate is irregular, with many smaller folds and curves, but only five of these appear large enough to be epispires. Like the previously discussed plate, it also has an epispire that is much larger than the others, with a length of 1 mm. The plate has little relief; both part and counterpart appear to be concave. This suggests that the position of this plate was lower on the theca than the previously described plate.

Discussion

It is probable that these plates belong to a specimen of *Gogia* or a *Gogia*-like ancestor, but it is not discountable that these may be edrioasteroid plates or plates belonging to some other early echinoderm. While *Camptostroma* also has epispire bearing thecal plates, the plates found in the Montenegro formation are much larger and show much lower relief (see section on *Camptostroma* herein). Similar plates found in the overlying lower member of the Poleta Formation are found in association with oral frame plates nearly identical to those of *Totiglobus lloydi*, an edrioasteroid from the Middle Cambrian of Nevada (Bell and Sprinkle 1978). However, the theca of *Totiglobus* is composed entirely of tightly sutured plates devoid of ornamentation or epispires, so the co-occurrence of epispire-bearing plates and oral frame plates is taken to be evidence of the presence of two types of echinoderms, and is used to infer here that these plates are more likely to be *Gogia* plates.

The material presented here is representative of the best-preserved echinodermal material found in the Montenegro Member of the Campito Formation. While preservation of these echinoderms does not permit description, or even a definite taxonomic assignment, they nonetheless represent the earliest unequivocal worldwide occurrence of skeletized echinoderms.

Lower Poleta Formation Plates

Shaly intervals within the carbonate-dominated Lower Poleta Formation preserve the remains of an echinoderm or echinoderms of uncertain origins. The rocks are Lower Cambrian, and also contain the remains of the biostratigraphic indicator species

Nevadella. No articulated plates have yet been discovered, but single isolated plate elements cover bedding surfaces, and in some cased, comprise limy lenses within these shaly intervals. Sprinkle (1973) first discussed these plates, but in the 22 years since their first publication, several forays into the White-Inyo Mountains by J. Wyatt Durham, James Sprinkle, and the author have yet to bear out the discovery of the animals that left these skeletal elements.

There are several morphologically differentiated varieties of plates, some of which are nearly identical to those plates found in *Gogia,* which justifies their inclusion here. The most common plating type is polygonal with pustulose ornamentation and epispires, which were noted by Durham (1978) to bear a resemblance to the thecal plating of *Gogia ojenai* (Figure 4.8). These plates are convex outward, and are found in different sizes and with different lengths of epispires, suggesting variable positions upon the thecal surface. Furthermore, overturned plates are present, identifiable by the same shape, concavity, and lack of ornament. The largest of these plates are 5 mm wide, and bear as many as 25 epispires.

A second type of plating is composed of a pustulose portion flanked by a groove-bearing portion. These grooves are aligned parallel to the boundary between plate morphologies, and have small pits between them. These pits are interpreted to be ligament pits first described by Paul and Smith (1984) to close the ambulacral coverplates, while the deeper grooves accommodated the ampullae of the tube-foot portion of the water vascular system (Figure 4.4). These are unequivocal oral frame plates of an edrioasteroid, and are nearly identical to the oral frame plates of *Totiglobus nimius* (Bell and Sprinkle, 1978).

SYSTEMATIC PALEONTOLOGY

PHYLUM ECHINODERMATA de Bruguière, 1791

SUBPHYLUM BLASTOZOA Sprinkle, 1973

CLASS EOCRINOIDEA Jaekel, 1918

FAMILY EOCRINIDAE Jaekel, 1918

GENUS GOGIA Walcott, 1917

Etymology – Named for Gog Lake in Mount Assiniboine Provincial Park, British Columbia, Canada. This is the type locality for the type species of the genus (Walcott, 1917b; Sprinkle, 1973).

Type species – *Gogia prolifica* Walcott, 1917; from the lower Middle Cambrian Mount Whyte Formation (*Plagiura-Poliella* zone) (Walcott, 1917b; Sprinkle, 1973).

Diagnosis – The generic diagnosis follows from the redescription of the genus carried out by Sprinkle (1973). There is not sufficient disparity in the Early Cambrian representatives of this group to warrant redescription of the phylum. However, redescription of the genus may soon be called for based on new undescribed specimens from North America and abroad.

Eocrinoids with an irregularly plated theca bearing epispires, a plated attachment holdfast, and multiple brachioles radiating from the oral surface. Thecal plates are polygonal and vary in size. Epispires are found either upon the entire surface of the theca or restricted to the oral surface. Brachioles, which number between 3 and 45, have biserial plating and 1 to 2 sets of covering plates. Brachioles are either straight or spiraled, always in a left-handed fashion. Brachiolar plates are arranged in a biserial

"zig-zag" pattern, with 1 to 2 pairs of covering plates per brachiolar plate. Mouth is central on the thecal summit, with 3 to 5 ambulacral areas leading to spout-like projections upon the edge of the oral surface upon which the brachioles were mounted. Hydropore and gonopore are unknown; anal pyramid is found in the CD interray or in a lateral position on the theca (Sprinkle, 1973).

Discussion - Sprinkle (1973) argued that the brachioles lacked an extension of the water vascular system, and that all brachiole-bearing blastozoans probably fed using mucous or ciliary extensions from the brachiole. The brachioles of *Gogia* are branches of the ambulacral system, as shown by the biserial nature of the brachiolar plating. Soft tissues and skeletal tissues of the ambulacral system of all echinoderms are biserial in nature, as the growth of the vessels of the water-vascular system is coincident with the skeletal framework of the axial skeletal system (Mooi and David, 1997). The lateral water vessel branches in an asymmetric biserial pattern, accounting for biserially arranged ampullae and tube feet. The axial skeleton then is forced to grow in a manner that accommodates these soft tissues, which accounts for growth mediated by the octet rule of Mooi and David (1997) and the subsequent biserial skeletal morphology. Brachioles are vertical branches of the ambulacral system, which is part of the axial skeleton. As these branches show the same biserial alternation of plates, and as skeletal biseriality is forced by biseriality of the water vascular system, it then follows that brachioles housed extensions of the water-vascular system.

GOGIA SP. A

Holotype – UCMP D-4700.

Occurrence – Upper Poleta Formation, Olenellus A subzone of the *Bonnia-Olenellus* zone, Early Cambrian, Westgard Pass Area of the White-Inyo Mountains, California.

Diagnosis – *Gogia* with large brachiolar plates relative to thecal plate size.

Description –Peter Guth, then a student at Deep Springs College, and Wyatt Durham of the University of California collected a part-counterpart pair of three incomplete Gogia specimens in 1971 (Figure 4.9). The three are in various stages of growth and decay, and all are preserved only in part. The largest and best preserved of these specimens has only a preserved upper theca and disorganized oral surface, and lies adjacent to a brachiopod, which it may have been attached to. What remains of the theca is 9 mm wide, and only about 5 mm long. The lower portion of the theca ends abruptly, with the beginnings of curvature indicating tapering along the edges, suggesting the animal was much longer than is indicated by this partial specimen. Two other nearby fragments are portions of the theca and brachioles, and may be fragments of the same individual splayed out on the original sedimentary surface. Very few small (1 mm wide) epispire-bearing thecal plates are preserved near the base of the remains of the specimen. The oral surface on one side of the specimen is undecipherable, while the counterpart, which bears wide swaths of glue used to repair the specimen, has the trace of an ambulacral area roofed by two rows of biserial cover plates.

This unnamed species has brachioles spiraled in a left-handed fashion. The largest specimen shows a 15 mm long brachiole, with an amplitude of approximately 1 mm, which makes the brachioles appear twisted, rather than coiled. At least two brachioles have a common origin. For each biserially arranged brachiolar plate there are

two cover plates. There are seven brachioles preserved, but there were likely more that were lost during taphonomy. Other *Gogia* fragments upon the same slab include a cluster to four brachioles attached to a skeletal fragment, two brachioles attached to a smaller skeletal fragment, and an unidentifiable skeletal fragment with brachiolar plates draped across the surface.

The author collected a second example of this animal in the summer of 2002, at the locality that bore the original find. The specimen is barely discernable as an echinoderm, but shows parts of two brachioles, indicating that it is probably the same species as the first, but sheds no further light on the organism.

Discussion - This Gogia comes from the lowest stratigraphic interval that bears articulated albeit incomplete *Gogia* specimens is the Upper Poleta Formation, *Olenellus* A subzone of the *Olenellus* Trilobite Zone, Lower Cambrian of the White-Inyo Mountains of eastern California. The remnant of the coverplate-roofed ambulacral area is the best evidence that any of the Early Cambrian *Gogia* species had a coverplate series and ambulacral construction similar to that found in the helicoplacoids, later edrioasteroids, and *Camptostroma*. The specimens represented upon this part-counterpart pair are each preserved in part, and may represent an individual that has been preyed upon. The top of the theca, two brachioles attached to a small thecal fragment, and a set of four brachioles attached to a thecal fragment appear to belong to a specimen that has been torn apart by a predator that exposed soft tissues inside the theca. The close proximity of these unique fragments and the brachiopod the animal may have been attached to support this hypothesis.

GOGIA OJENAI Durham, 1978

Holotype – UCMP 14526

Occurrence – Lower Cambrian Latham Shale, *Bristolia* subzone, *Bonnia-Olenellus* Zone, Marble Mountains, San Bernardino County, eastern California.

Diagnosis – *Gogia* with globular, almost spherical theca, with short holdfast made of small plates with rounded tips, and a flared distal suction attachment pad. Thecal plates have concentric radiating ridges with several small medial bumps. Epispires are found in the upper half of the theca. Spiraled brachioles are numerous, with two cover plates per brachiolar plate (Figure 4.10).

Description – This is currently the best-preserved and most complete *Gogia* from the Early Cambrian. The specimen was originally collected by Mr. Morris Ojena, and then passed along to J. Wyatt Durham, who described the species (Durham 1978). Theca is large and nearly spherical, with a width of 17 mm, and a height of 17 mm. The theca ends at a tapered holdfast, which is composed of many small hemispherical to sub-hemispherical plates of nearly the same size, but uniformly small. The holdfast is 6 mm long and 2 mm wide, with approximately 20-25 plates encircling the holdfast, flaring to an attachment pad 5.5 mm wide. The plates at the top of the attachment pad are larger than those at the base. The base of the holdfast terminates in a slightly invaginated pad. The holdfast extends summit-ward toward the theca, at the base of which the small rounded plates of the holdfast abruptly disappear. Plates near the base of the theca are of a similar size as the holdfast plates, but have deep pustules upon the surfaces. These plates grade into larger plates that show pustules medially, and ridges distally. The relief

is roughly the same as the relief upon the smaller plates, but the larger plates have more laterally extensive ornamentation. These smaller ornamented plates grade into larger epispire bearing plates, with the transition nearly complete roughly half of the distance between the holdfast and the summit. The largest of these plates is 2 mm in width. Epispires vary in size; some plate junctions do not bear epispires at all. The largest epispires are approximately 0.3 mm in length. The largest plates have as many as 15 central pustules, with distal ridges radiating out from the central region. Large medial plates have smaller epispires, while summit-ward plates have deeper epispires. Medial plate epispire count varies from 10-12 for larger plates. The deepest epispires are found upon plates at the summit itself, which can be assumed to be plates of the oral surface. The specimen has been crushed, making recognition of the fine details of the oral surface and boundary between the oral and thecal surfaces difficult to discern. Oral plates are approximately 1 mm wide at the largest, with fewer epispires, varying from six to four. These plates have little ornamentation, with as few as one to two pustules, with concave relief to the plate. This gives the epispires wide flanges.

The brachioles are very well preserved, despite poorly preserved ambulacral areas. There are at least 14 brachioles preserved whole or in part, the longest of which is 23 mm long. The brachioles are spiraled in a left-handed fashion. Durham observed that in 15 mm, the brachioles made six complete spirals (Durham, 1978), for an average of 2.5 mm per complete spiral. Spirals are coiled more tightly distally than proximally. The brachioles vary in both wavelength and amplitude. Wavelengths as short as 4 mm and amplitudes of as wide as 2 mm are found in the tightly coiled distal end of the longest

preserved brachiole, while longer wavelengths of approximately 9 mm and shorter amplitudes of 1 mm are found in brachioles nearer the summit.

Brachioles are composed of biserially arranged brachiolar plates, some of which show stereom. One brachiole in particular appears malformed; it is biserial proximally, and becomes uniserial more distally. The commissure between the brachiolar plates is a diagonal line rotated approximately 10 degrees away from the brachiolar midline (Figure 4.11). Another brachiolar plate shows at the base a linear series of three modified brachiolar plates that lock the brachiole into the ambulacral area. Two larger polygonal plates that effectively widen the base of the brachiole at the point of insertion in turn underlie these three plates. The brachioles are roofed by interlocking convex-outward coverplates. There are approximately two cover plates per brachiolar plate.

Cross sections of proximal brachiolar plates show biserial articulation at the bottom, and a central cavity enclosed entirely by the brachiolar plate (Figure 4.9). This is homologous to the cavity named the median canal recognized in the brachioles of *Gogia longidactylus* by Sprinkle (1973). The cavity found in *Gogia ojenai* is much larger, which is probably due to its proximal position. The canal likely gets smaller distally, as the brachiolar plates get smaller. The lateral faces of the brachiolar plates have a concave groove leading to the median canal.

Discussion - This is the first and still best preserved representative of the genus *Gogia* from the Early Cambrian of North America. The detail preserved in the brachioles and aboral areas is without equal in the group. The distal portion of the holdfast is intact, despite becoming detached from the substrate. Unlike other specimens, this individual shows the flexible sheet of small plates that served as the attachment surface. The part

and counterpart pair when taken together show that the counterpart preserves the outer edge of the distal tip, while the part preserves the invaginated interior, which because of its invaginated nature shows the structure to have been flexible. Taken with other evidence from other members of the group, this supports the theory that *Gogia* attached to hard or semi-lithified substrates via attachment by a suction pad. The holdfast is similar in many ways to those described in the new species described herein, *Gogia lockeri*, as well as the Middle Cambrian species *Gogia granulosa* and *Gogia spiralis*, which has been found attached to trilobite debris (Sprinkle, 1973).

The brachioles of this species are spiraled, but have varying wavelengths and amplitudes. The brachioles directed upward off of the theca show a lesser degree of coiling than do the brachioles that branch off to the side of the theca at a right angle, which show much tighter coiling. The variation found within the same individual suggests that brachioles were capable of expanding and contracting the brachioles though tight versus loose coiling. The purpose for this may have been to avoid clipping by predators, or to bring food particles closer to the mouth. The latter explanation is more likely as brachioles had very little soft tissue, and would therefore not have been a good nutritional source. These brachioles are similar in coiling variability to the brachioles found in other Early Cambrian coiled brachiole forms, most notably *Gogia fowleri*, discussed herein.

The well-preserved brachioles in this specimen did not entirely avoid the ravages of taphonomy; some broken off, exposing in one case a cross-sectional view of the interior of the brachiole. The base of the brachiole shows the suture between articulating biserial plates, and the subsequent relief difference created by the biserial nature (Figure

4.9). Above these biserial plates is a large central cavity, which is roofed by plating that forms the floor of the brachiole. The aforementioned concave grooves allowed for the passage of tube feet from the radial water vessel, which lay inside of the groove. The biserial nature of the brachioles suggests that these structures are derived from the ambulacral system from which they feed into. As ambulacral areas have biserial skeletal plating to accommodate an alternately branching water vascular system, it follows that the brachioles must have also housed the water vascular system, and therefore tube feet employed in the service of food gathering.

GOGIA FOWLERI n.sp.

Etymology – Named in honor of Ed Fowler, the collector of the holotype specimen.

Holotype – UT TMM 2047TX1a, UT TMM 2047TX1b

Occurrence – Early Cambrian Latham Shale, *Bristolia* subzone, *Bonnia-Olenellus* zone, Providence Mountains, San Bernardino County, California.

Diagnosis – *Gogia* with plates bearing 0 to 3 medial angulations upon the surfaces, and edges lacking epispires. Spiraled brachioles, a short holdfast composed of small rounded plates. Theca bulb-shaped (Figure 4.12).

Description – Small specimen, 8 mm wide, and 9 mm long. Theca wide near summit, tapering near holdfast. Near summit, theca is composed of large unornamented polygonal plates that were tightly sutured. Few epispires are found along the edges of these, which may be an ontogenetic variation. Largest plates are a maximum of 1 mm in width. Plates are convex outward in profile.

The size of individual plates changes roughly 3 mm away from the summit. Larger plates give way to a row of smaller polygonal plates, roughly 1 mm in width. Diagnostic of these is a small angulation near the lower edge of each plate. The next plate row below these is comprised of smaller polygonal plates yet, with a width of approximately 0.6 mm. These have the same diagnostic angulation, which occurs in the center of the plate. Below this plate row, plate size and dimensions diminish, as the theca grades into the holdfast. Holdfast plates are multi-sized, and many individual plates have a large angulation.

The holdfast of this particular specimen is recumbent upon the theca due to crushing during taphonomy. The holdfast is 6 mm long and approximately 1 mm wide, and terminates in an upward facing circlet of plates. This termination is flared to approximately 1.5 mm. Inside the circlet are approximately 6+ radially arranged lath-shaped plates. It appears that the lower surface of the holdfast has been removed, exposing the interior.

The summit of the theca has a single incompletely preserved brachiole. It extends 6 mm to the left of the theca, and ends abruptly, where it was most likely broken off during taphonomy or the activity of scavengers or predators. The base of the brachiole is composed of biserially-arranged plates, each of which is roughly 0.5 mm in length. Coverplates are only exposed near the end of the brachiole. Coverplates are "L" shaped, with the leg of the L pointed inward toward the brachiolar groove, where, when closed, they served to roof the groove. There is one cover plate per brachiolar plate.

A single oral plate is found upon the surface of badly crushed counterpart. This plate, found near the summit, has deeply incised grooves, presumably for the passage of

tube feet, or owing to their large size, perhaps brachiolar attachment. It is possible that this plate is an epispire-bearing thecal plate, but because of the size of the specimen and lack of other epispire bearing plates, this is not as likely a scenario. A poorly preserved anal pyramid is present, just below the edge of the theca. Six radially arranged lath-shaped plates fill a cavity that is incused into the theca. This probably occurred during the crushing of the specimen during burial. The plates surrounding the anal pyramid lack epispires.

Considering the small size of the specimen, and the overall paucity of epispires upon the theca and oral surface, this specimen was most probably a juvenile that had yet to develop epispires in response to respiratory stress brought about by a decreased surface area-to-volume ratio. The position of the anal pyramid designates the surrounding surface as the CD interray, but ambulacral plating is not visible. Surface plates show stereom.

Discussion - Growth in *Gogia* follows the tenets of the Extraxial-Axial Theory of Mooi and David (1997), in that there are separate zones of growth, with new plate addition at the boundaries of each zone and plate growth away from these zones (Figure 4.13). This particular specimen has a well-preserved boundary between the imperforate and perforate extraxial regions, however, the boundary is not at the base of the theca as has been proposed by Sprinkle and Guensburg (2001), but rather, midway between the top of the holdfast and the summit. An angulations found upon plates of the holdfast are also found in successive plate rows extending toward the midline of the theca. The angulations are of uniform size in all plates that bear it, although the size of the plate bearing the angulation increases towards the thecal midline. This suggests that plate

generation occurs near the base of the holdfast, with plates growing larger away from the base. Near the base of the theca, plates grow larger laterally, by adding new plate material to the edges of the plate. The last plate row associated with the imperforate extraxial region has an angulation that is near the lower edge of the plate, suggesting that imperforate extraxial plates increase in width more readily toward the top of the plate.

GOGIA INYOENSIS N. SP.

Etymology – Named for Inyo County, eastern California, where this and many other Early Cambrian echinoderms have been found.

Type Material – Holotype, UT TMM 2043TX1a, UT TMM 2043TX1b; Paratypes, UT TMM 2043TX2, UT TMM 2044TX1.

Occurrence – Siltstone and mudstone beds near the top of the Gold Ace Limestone Member, *Olenellus* A subzone, *Bonnia-Olenellus* zone, Early Cambrian Carrara Formation, Emigrant Pass area of the Nopah Range, Inyo County, California.

Diagnosis – *Gogia* with radiating spoke-like ridges on surfaces of thecal plates, with medial pustules. Thecal plates are very large (up to 5 mm in width); theca wider at summit, tapering to holdfast at lower end. Overall bulb shape to theca. Holdfast plates are large at proximal end and smaller distally. Epispires and therefore perforate extraxial region confine to upper half of theca. Specimen shows long spiraled brachioles.

Description – UT TMM 2043TX1a: Relatively complete, large, crushed specimen; theca is 18 mm long (not including the holdfast), and 13 mm wide. The holdfast is incomplete, but was at least 5 mm in length (Figure 4.14). At least eight large plates comprise the visible portion of the theca; two show pustulose ornament, but this is

probably due to weathering of the original plate material. The moldic fossil has an imprint of the plate ornament preserved as a thin layer covering a cavity formed from the impression of the plates; however this has begun exfoliating. Plates are large, with small epispire pores along the edges. The epispires are not wider than 0.67 mm, and not generally longer than 1 mm in the largest plates near summit. These have a radius of 5 mm, with as many as 18 V-shaped epispires per plate. Plates are polygonal; one is roughly rectangular in outline, while another is pentagonal. The center of the plate rises to a small summit, which is adorned with small pustules at center of plate, with as many as 35 ridges radiating to the edges of the plate. Two plates toward summit on left side of specimen are articulated as in life position. The V-shaped epispires face one another, forming a rhombus shaped pore, 2 mm in length, 0.5 mm in width. The remainder of this particular commissure is straight and tightly sutured, without any other visible pores.

Two incomplete plates preserved upon the counterpart of the specimen are representative of the plating of the oral surface. The first of these is 2 mm wide, with a single deep V-shaped groove with raised edges incising the plate edge. The second is not in-situ, but it is clearly differentiated from the plating of the theca. Despite being incorporated into the disarticulated holdfast of the specimen, it is clearly similar to the perforate extraxial plating of other eocrinoids.

Ten brachioles radiate from the summit. The longest of these, and probably the best representative of the length, is 28 mm long. On this brachiole, the wavelength is 3 mm, and an amplitude of 1 mm. A second brachiole, preserved only on the counterpart of the specimen has a wavelength of 1.5 mm and an amplitude of 1 mm (Figure 4.15). Plates appear to be larger proximally and smaller distally, but this is difficult to quantify,

as distal portions are poorly preserved. Brachiolar plates are biserially arranged, with interlocking pentagonal plates typical of the genus. Brachiolar plates are small, with one brachiolar cover plate per brachiolar plate. Cover plates are small and lath shaped.

The holdfast is small, and is preserved only most proximally. It is composed of small conical plates or slightly larger sub-hemispherical plates. Further away from the theca, plates become disorganized.

Overall, the specimen is crushed, with the visible side of theca caved in. The specimen is more or less complete, despite the oral surface missing due to orientation of specimen when buried, and lower portions of the theca missing because of a chip of rock that was not replaced when a crack in the specimen was repaired.

Discussion - This specimen has brachioles that, similar to those found in *Gogia ojenai*, are preserved at different degrees of expansion and contraction. This suggests that this species of *Gogia* as well used spiraling as a means of retracting the brachioles in toward the theca. The holdfast of this species is poorly preserved, but shows a disc-like lower attachment pad, similar to that of *Gogia fowleri*. The fundamental difference is in the presence of much larger plates making up the distal tip of the holdfast, and larger ornamented thecal plates. As few as six to seven plates make up the diameter, while in other species with a comparable theca size this number is as high as 20. There is no pustulose ornament, but each plate does have radiating ridges that ultimately form the borders of the epispires along the plate edge.

This new species is confined to the uppermost siliciclastic beds of the Gold Ace Limestone. The Pyramid Shale overlies these rocks. The rocks are similar lithologically, but there is a drastic faunal change, delineated by the presence of *Nephrolenellus*

multinodus in the Pyramid shale. Furthermore, lisengang banding is more prevalent in the overlying Pyramid Shale.

UT TMM 2044TX1: This specimen is large but incompletely preserved in part and counterpart, 19 mm at the widest point, and was perhaps as long as 25 mm in length, discounting the holdfast (Figure 4.16). The theca is missing the basal-most portion, but enough remains to indicate that the lower portion was tapered. What little remains of the holdfast was exposed only after acid etching of the specimen, which exposed six small rounded plates at the base of the theca on only one side of the specimen.

The theca is comprised of a small oral surface at the summit, and a more extensive system of large tessellate plates making up the body wall. The circumference of the theca is accommodated by possibly seven of these large plates, each of which is four to six millimeters in diameter. Plates are extensively recrystallized, but acid etching revealed remnants of plate ornament. The large thecal plates show robust radiating ridges and small distal epispire pores. Thecal plates are concave outwards, and are tightly sutured.

The oral surface accounts for the tapered summit of the theca. The plating of the oral surface is composed of much smaller stellate plates, ranging in size from one to three millimeters in diameter. The epispires on these plates are deep, extending to near the center of the plate, with raised edges. One plate in particular has the overall appearance of an asterisk (*) with six epispire grooves extending a third of the plate diameter toward the center of the plate. Larger plates are nearer the midline with the lower theca, while smaller plates are near the summit.

Three ambulacra are preserved on the counterpart, while none are preserved on the part. The ambulacra are incomplete and poorly preserved. Of the three, the left-most is the most complete, showing distal branching. This is the likely reason for the large number of brachioles in this specimen, as at least six brachioles extend from the distal portion of this amb alone. Proximally, ambulacral cover plates are large, and grow smaller distally, suggesting growth moderated by the octet rule (Mooi and David, 1997). The distally branching ambulacrum shows at least two sets of bifurcations, which resulted in four food grooves distally from a single ambulacral branch. The middle and right-most of the three ambs are detached distally from the oral surface, suggesting that the amb may have been able to grow free of the theca (Figure 4.17). The tips of small plates within the middle ambulacrum suggest biserial floor plating, but poor preservation delimits any definitive assessment of these plates.

Seven brachioles are preserved in part or in whole, the longest of which is 39 mm long and incomplete. The distal-most portion of this brachiole is draped over the surface of a trilobite hypostome. Brachiolar plates are biserial, with one coverplate per brachiolar plate. The brachioles are spiraled, with amplitudes varying from approximately half to one millimeter, and wavelengths varying from 4.5 mm to approximately 9 mm.

Discussion - The ambulacra in this specimen are the best examples seen in the Early Cambrian record of *Gogia*. They appear to branch free from the edge of the theca, which is undocumented in this group. Paul and Smith (1984) argued that this happened in the lepidocystids, which was the first evolutionary step toward the development of crinoid arms, which house lateral branches of the water vascular system. While the

author disagrees with the morphological interpretation of *Lepidocystis* in Paul and Smith (1984), the theory is likely the correct pathway to toward the development of crinoid arms, but may have occurred in taxa other than the lepidocystids. Considering the Middle Cambrian appearance of the first crinoid *Echmatocrinus* from the Burgess Shale (Sprinkle, 1973), the growth of the ambulacra off of the oral surface must have occurred early in the record.

UT TMM 2043TX2 - Amateur collector Ed Fowler collected a single poorly preserved juvenile specimen of *Gogia inyoensis* in a shaly interval within four to five meters of the top of the Gold Ace Limestone Member, *Olenellus* Zone of the Lower Cambrian Carrara Formation. There are remnants of spiraled brachioles, some of which have a few coverplates preserved, and a highly weathered partial theca. The specimen is 10 mm in height and 8 mm in width, which makes it much smaller than the other articulated specimens of *Gogia inyoensis*, with which it shares the same holdfast plating and thecal plate ornamentation. The plates that comprise the holdfast are of two distinct sizes, while the thecal plates bear small pustules and ridges.

Discussion - This specimen establishes that the diagnostic traits of the species are not found only in individuals at a particular to a particular ontogenetic stage, but occur throughout the life cycle. The presence of these diagnostic characters also establishes that other specimens devoid of plate ornament from the overlying Pyramid Shale are not merely juvenile *Gogia inyoensis* individuals sans the emergent characteristics of the adult form of the species.

Disarticulated Plate Material - The siliciclastics of the Gold Ace limestone also preserve single large thecal plates that are diagnostic of the new species *Gogia inyoensis* (Figure 4.18A). One of these plates is six millimeters across, and better preserves the plate ornament than any thecal plate in any articulated specimen. The plate is convex-outward, with ridges radiating outward from the apex in the center of the plate. Some of these share a common origin at the center of the plate and radiate toward the edges, while other ridges are arranged into parallel sets of ridges that originate a short distance away from the apex. There is minor pustulose ornamentation distally between these sets of radiating ridges, and also interspersed between ridges in the proximal portion of the plate, but none on the central umbo of the plate, delineating it from *Gogia ojenai*-type plating. There are also many more parallel ridges in this species than in any other. The plate edge is cut by many indentations, which are difficult to count because of preservation, but may have numbered in the twenties.

Another large epispire-bearing plate from the same horizon was preserved inverted (Figure 4.18B). The six millimeter wide plate is concave inward, suggesting that the plate is overturned. The interior is smooth, with two smaller skeletal fragments resting upon the surface. Along the plate edge are 22 epispire grooves, each of which is roughly 0.5 mm deep.

Additional plates exist from the Pyramid Shale that are smaller in diameter (four millimeter) but still bear deep epispires. Epispire grooves extend as far as one millimeter toward the interior of these plates.

Discussion - This first plate is interpreted to be a large thecal plate of the new species *Gogia inyoi*. The plates of the articulated specimens are weathered to the point

that plate ornamentation is obscured. There is enough of the pattern of radiating ridges preserved within one of the aforementioned specimens to suggest that these came from the same species. The disarticulated plate differs from plates found in *Gogia ojenai* in that they are 2-3 times larger than the largest plates found in the latter, and have an ornamentation pattern that emphasized radiating ridges over the pustules that figure so prominently in *Gogia ojenai*. The smaller plates are interpreted as oral surface plates, similar to the asterisk shaped plates found upon the oral surface of the larger specimens of this species.

GOGIA LOCKERI n.sp.

Etymology – Named in honor of Carl Locker of Healdsburg, California, who collected and donated the holotype.

Holotype – Holotype, UT TMM 2045TX1; Paratypes, UT TMM 2945TX2, UT TMM 2945TX3.

Occurrence – Siltstones and mudstones near the base of the Pyramid Shale Member, *Nephrolenellus multinodus* subzone, *Bonnia-Olenellus* zone, Lower Cambrian Carrara Formation, Emigrant Pass area of Nopah Range, southeastern California.

Diagnosis – *Gogia* with unornamented thecal plates, short holdfast with flared distal tip, uniformly sized small holdfast plates. Spiraled brachioles with two coverplates per brachiolar plate.

Description – Holdfast is short (three millimeter long in holotype, or 23% of total height), with a two millimeter wide stalk that flares to three millimeter wide at the distal tip. Holotype shows 13 brachioles, while a larger incomplete specimen shows 15; an

unequivocal juvenile shows none, and a poorly preserved fourth specimen has only three remaining brachioles.

Discussion – This new species differs from *Gogia ojenai* in that it has unornamented thecal plates, and is generally smaller, with a theca that is 10 mm wide, and 13 mm long, including the holdfast, although this may be due to the fact that the type specimens are likely juveniles. Development of epispires occurs later in ontogeny, but plate ornamentation exists at the center of any juvenile plate of individuals that bear ornament, as plates grow by adding new material to the edges. It is similar to *Gogia ojenai* in thecal outline and in the flared distal tip to the holdfast. The two species also share a common holdfast structure, which is similar to the holdfast found in *Gogia spiralis* (Sprinkle, 1973), which has been found attached to trilobite debris. Both early Cambrian species have a relatively short holdfast made of small multi-sized plates, which is flared at the distal end, presumably for attachment to skeletal debris, similar to the manner described in the discussion of *Gogia fowleri*. A poorly preserved specimen pressed onto the glabella of an *Olenellus* trilobite cephalon supports this premise.

The variability found in the coiling of two brachioles within the same specimen again suggests that brachioles were able to reduce the length extended from the theca by coiling. By increasing the amplitude of the coiling, the brachioles decreased in wavelength, which drew the brachiole inward toward the thecal surface. When actively feeding, the brachiole wavelength would have been increased, extending the brachiole into the water column. This is likely to have been an anti-predatory response, or it may have aided in bringing food particles from the distal tips of the brachioles closer to the ambulacral areas.

Descriptions of the type specimens follow.

UT TMM 2045TX1: The holotype specimen of the new species *Gogia lockeri* is a part and counterpart pair on a slab containing a second less well preserved part-counterpart pair of the same animal. This particular specimen was collected by Carl Locker of Healdsburg, California, and sent to the University of Texas for study.

The theca of this specimen is small and globular (Figure 4.19), with a width of 11 mm, and a height of 12 mm, from the tip of the holdfast to the summit. The holdfast is relatively short at four millimeter, and is composed of small multi-sized hemispherical to conical plates, which are approximately 0.25 mm wide. The holdfast tapers to 2.5 mm in width, then widens to four millimeters at the tip. Proximally, holdfast plating yields to thecal plating 1.5 mm toward summit.

Thecal plating near the holdfast is comprised of small unornamented tessellate plates with shallow to absent epispires, which grow as large as two millimeters wide, but are generally smaller. Plates are slightly convex outward, with less relief than seen in other species, and epispires that are only a fraction of a millimeter deep. Plates grade into larger epispire-bearing plates toward the summit; the epispire edges are marked by raised edges. Along the boundary between the imperforate extraxial region and perforate extraxial region there exists a single plate with as many as 12 epispires along the upper half of the plate, but none on the lower edge. In the second specimen, the shallow epispires of the medial thecal plates conjoin to form large pores (approximately one millimeter wide) with raised edges.

The oral surface is marked by a drastic decrease in plate size summit-ward, as well as tapering toward the summit. Oral plates are not convex in profile, but do have raised edges surrounding the epispire folds. Since they are much smaller is size (approximately 0.5 mm maximum), these plates have fewer epispires. The oral surface is more disorganized that the rest of the theca, which may be a result of the greater amount of soft tissue required to ligature smaller plates and the subsequent ravages of taphonomy.

The ambulacral system is preserved only as three raised areas on one side, and two more on the counterpart. Diagnostic features such as the anal pyramid and 2-1-2 arrangement of ambulacral areas are not preserved, so it is impossible to assign the ambulacra Carpenter designations. There are at least 11 coiled brachioles in various states of preservation, the longest of which is 10 mm. A single well-preserved coiled brachiole shows a wavelength of 2 mm and an amplitude of 1.5 mm, while another more poorly preserved brachiole shows a wavelength of 4 mm and an amplitude of 0.5 mm. The brachioles are arranged in clumps around the raised areas taken to be ambulacral areas. One such clump appears to have portions of seven separate brachioles preserved, suggesting that the animal may have had as many as 35 brachioles in life. Coverplates are absent in many places along the brachioles, but enough are present along some stretches to establish a ratio of 2 coverplates per brachiolar plate.

UT TMM 2045TX2: This slab of rock houses two specimens; one juvenile and a second more mature but somewhat incomplete specimen. The more mature specimen (Figure 4.20) is 10 mm wide at the widest point, and 11 mm long, not counting the

holdfast, which is incomplete and recumbent upon the lowest portion of the test. The theca is inverted conical in shape, with a rounded top. The holdfast is composed of small (<< one millimeter in diameter) uniformly sized plates with rounded ends. Thecal plates are larger medially and grade into smaller plates toward the lower pole. The largest plates are approximately two millimeters in diameter. Epispires on the largest medial plates are numerous but not very deep; as many as 12 epispires are found in a single large plate, but none are deep. Two plates from further toward the summit are found lying next to the theca; a single upper thecal plate is found in situ. These plates are highly asymmetric, with large deep epispires with raised ridges along the edge on the side of the plate toward the summit, and absent on the side oriented toward the lower pole. One of these plates has as many as four epispire grooves on the upper third of the plate, with grooves extending nearly one 6^{th} of the plate length. Three relatively well-preserved brachioles extend from the summit, each of which is less tightly coiled proximally than distally. Three more brachioles are found to the left of the specimen, but are obscured by debris, and may possibly not belong to this animal. The specimen is highly oxidized, obscuring detail, especially in the brachioles.

The juvenile specimen (Figure 4.21) is much smaller, with a width of five millimeters, and a height of nine millimeters, three millimeters of which is accounted for by the holdfast. The holdfast is composed of small (<< one millimeter in diameter) uniformly sized plates with rounded knob-like projections. The theca tapers dramatically at the point of attachment of the holdfast, which is one millimeter wide. Theca is roughly spherical, and is composed of polygonal plates with straight edges, and lacking epispires. Plates are slightly larger than one millimeter in diameter, and lack ornament on the

surfaces. A single heavily oxidized brachiole spirals a short distance away from the theca to the right of the specimen before abruptly ending, probably broken off during taphonomy.

Discussion - The lack of epispires in this and all other juvenile specimen is because the minimal volume of a juvenile echinoderm does not necessitate extra surface area dedicated to respiration. As the animals grew larger, epispires formed in plates near the summit, and then developed in medial plates.

UT TMM 2045TX3: Summit of an incomplete specimen (Figure 4.22). Theca is 19 mm wide with brachioles evenly spaced along the edge of the entire theca. The outline of the theca is visible, and appears to be made up of large plates, but individual plate details are indistinct. The oral surface is composed of smaller plates, but is pyritized to the point that individual plates are difficult to make out. Fifteen spiraled brachioles are present, radiating outward from the edge of the oral surface. Once again, plating is pyritized, and it is therefore difficult to make out individual plates. All brachioles are straight proximally, and spiral distally. The longest brachiole is 12 mm, with roughly seven millimeters per coil. The third brachiole from the right shows biseriality. Brachiole on right is facing upward, with coverplates removed to show poorly preserved brachiolar groove. There appears to be three clumps of brachioles; the six on the right, five in the center, and four on the right. No evidence of an anal pyramid.

Discussion - The usefulness of this specimen lies in its gross anatomy, in that it has retained so many well-spaced brachioles. Also, the size of this specimen shows that this species did grow to be at least as large as *Gogia inyoensis* and *Gogia ojenai*. The

best-preserved specimens of this species are juveniles at different points in ontogeny, but do differ in anatomy from the juvenile specimen of *Gogia inyoensis*. The different stratigraphic interval at which these *Gogia* are found follows the pattern of previously described Middle Cambrian *Gogia* which are found to have a single species occurring at each known locality (Sprinkle, 1973), showing dominance of each particular morphotype per geographic and temporal interval.

Plasticity of the brachioles in this specimen as well as in others supports the premise that brachioles were retractable. This specimen was collected by Carl Locker of Healdsburg, California, who sent it to Lloyd Gunther of Brigham City, Utah, who then sent it on to the University of Texas at Austin for study in 1985.

UT TMM 2045TX4: Poorly preserved specimen with pitting upon surfaces of plates, but no evidence of plate ornament (Figure 4.23). No brachioles, epispires difficult to see, but possibly exist near the summit. Overturned *Olenellus* cephalon lies on top of the lower portion of the theca of the specimen.

Discussion – The proximity of the trilobite cephalon strongly suggests these *Gogia* attached to skeletal fragments, as do the Middle Camrbian species, *G. spiralis* and *G. hobbsi* (Sprinkle, 1973). The lower attachment pad found in other specimens of this species suggests that these organisms attached by means of suction.

GOGIA MCCOLLUMI nov.sp.

Etymology – Named for Michael McCollum of Spokane, Washington, who collected and donated the specimen.

Holotype – UT TMM 2046TX1

Occurrence – Saline Valley Formation, *Bonnia-Olenellus* Zone, Lower Cambrian, Esmeralda County, western Nevada.

Diagnosis – Inverted conical theca, without change in profile at the transition from thecal to holdfast plating (Figure 4.24). Lower half of the theca composed of small multi-sized plates bearing conical projections. The upper half of theca is composed of flattened unornamented plates with deep epispires. Brachioles are spiraled in a left-handed fashion.

Description – The conical theca is 15 mm in height, and is seven millimeters in width at the summit, tapering to a point. Theca divided into two distinct portions indicated only by change in plate morphology rather than tapering so prevalent in other groups. The lower holdfast is six millimeters in length, with the external surface preserved. Holdfast composed of two different sized plates, the larger of which are approximately 0.67mm in diameter with a medial knobby projection. Roughly hexagonal or pentagonal in outline, some are fringed by smaller secondary plates, which fill gaps between larger plates. The tip of the holdfast is composed of an array of smaller plates. The holdfast is similar to an undescribed probable pyramidal eocrinoid from the Carrara Formation.

Upper portion of theca is nine millimeters in length, and is composed of large stellate epispire-bearing plates. Some show minor variation in size, with larger plates near the holdfast, and smaller plates near the summit. Smaller plates have as few as six epispires, while larger plates have as many as 10-12. Epispire bearing plates are directly

adjacent to the knobby plates of lower theca. There are a total of parts of eight large plates present, and parts of five smaller plates.

The oral surface is composed of small plates approximately one millimeter in thickness at the summit of the specimen. These summit plates have become disarrayed during taphonomy.

The brachioles are at lest as long as 14 mm, but each is incomplete. Four brachioles are present, with two each at each corner of theca. Brachioles are spiraled, but the right pair of brachioles begin spiraling four millimeters away from the theca. Both appear to begin with a slight right-handed spiral, then twist in the normal left-handed fashion distally. Brachiolar plates are biserially arranged and C-shaped in profile, presumably allowing space for passage of the water vascular system. The second brachiole from the right appears to have inter-plate pores, perhaps for ampullary compensation space. The coverplates are missing. Further evidence of the water vascular system extending into the brachioles is shown at the point of articulation of the brachioles with the theca, which shows large modified ambulacral plates at the junction, which appear to be floor rather than cover plates. The brachioles on the right side of the specimen share a plate at point of articulation with theca. Aside from these recognizable plate types, the oral plating is a disorganized jumble of plates.

Discussion - The most diagnostic character of this taxon is the inverted conical profile of the theca. The holdfast, rather than being thin and cylindrical is conical, so that there is no apparent change in profile as the holdfast transitions into the plating of the theca.

GOGIA SP. B.

Holotype – UT TMM 2049TX1

Occurrence – Lower Cambrian Carrara Formation, *Bonnia-Olenellus* zone, Groom Range, Nye County, Nevada.

Diagnosis – This *Gogia* is known from two specimens upon a single small piece of limestone channel fill from the Lower Cambrian Carrara Formation, Groom Range, Nevada (Figure 4.25). The specimens are both preserved in the original calcite, retaining in some places cleavage faces diagnostic of the single crystal calcium carbonate skeletal elements of echinoderms. The theca of the first and larger of the two specimens is incomplete, as it is missing the entire lower attachment surface. What remains of the theca is 20 mm wide, and is composed entirely of large tightly sutured polygonal plates with straight edges. Other regions of the theca are absent or obscured in this specimen. The largest plates are five millimeters wide, and all plates present are moderately convex outward. A large medial cavity surrounded by inward-facing plates is exposed at a part of the theca that was crushed. Aside from the oral surface, the majority of which is covered, epispires are not present upon any part of the theca of this specimen. The proximal insertion points of three thickets of brachioles are present in this specimen, suggesting that the space between these three points is the oral surface. Despite this assertion, there are no epispires, and there is no change in plating relative to the theca below to indicate the different region. It appears the ambulacral areas that anchor the brachioles have grown out onto the surface of the theca.

The brachioles in this specimen are multitudinous; seventeen exist on the surface of the specimen, with an additional four in cross section along the edge of the rock.

Brachioles are arranged into three thickets. The left thicket contains three surface brachioles, the middle thicket contains nine, and the right thicket contains five. Positioning suggests that the thickets existed at the terminus of each ambulacrum. Brachioles are straight, and are arranged linearly, stacked atop one another in line with the ambulacrum. Each brachiole is composed of biserially arranged brachiolar plates, and overlapping cover plates. Brachiolar and cover plates are in a 1:1 ratio. The projections of the overlapping biserial coverplates would have covered the brachiolar groove when closed. None of the brachioles branch, but in the central thicket there appears to be a node from which the brachioles arise. Along the left edge of the theca lie five lath-shaped plates that protrude out of the surrounding matrix. Considering their shape and relative position upon the theca, these are interpreted as the plating of the anal pyramid. This would indicate that the left-most thicket of brachioles corresponds to the C amb; the central thicket is correlated with the B amb, and the right-most thicket is correlated with the A amb. This agrees with the relative spacing of the thickets, as B is closer to C than it is to A.

The second specimen lies draped over the aboral end of the larger specimen. All that is preserved of this smaller specimen is a circlet of four plates near the summit and a thicket of brachioles. The plates are polygonal, lack epispires, and are of maximum size of two millimeters. The thicket contains three brachioles; one extends to the left, and two overlapping brachioles extend upward. The brachiole toward the edge of the theca overlaps the brachiole directly below it near their respective bases. Past this point, it veers to the left and lies directly apposed to the brachiole below it, giving the false impression of a single thick brachiole This specimen is undoubtedly the same species as

the larger. It is notable that in this specimen as well there are no epispires near the aboral end of the theca or upon what little of the oral surface remains.

Discussion - These specimens show enough detail to indicate they are new species, but are too incomplete, especially in the aboral region, to warrant naming of these new specimens. Unique to these *Gogia* are the lack of epispires and straight brachioles. The former of these characters suggests these lived in a high energy well-aerated environment, which is supported by the limestone cobbles found in the formation.

Conclusions

1. Gogia is already the most diverse echinoderm from the Cambrian; with the addition of these new species and synonymization of many of the helicoplacoid species, it is also the most diverse Early Cambrian echinoderm group. *Gogia* is almost ubiquitous in Lower Cambrian strata, but because of their poor preservational potential they are rarely preserved.

2. The brachioles are interpreted here to have been retractable, and to have housed branches of the water vascular system. Pores between adjacent brachiolar plates appear to be compensation spaces for ampullae, which opened the brachiolar plates and kept the tube feet inflated.

3. In addition to *Gogia ojenai* Durham, 1978, and *Gogia (Alanisicystis) andalusiae* Ubaghs and Vizcaïno, 1990, there are four new named species, two additional new unnamed species, and possibly two other occurrences marked by the presence of *Gogia*-like plates. The new named species are *Gogia fowleri* from the Latham Shale of eastern California, *Gogia inyoensis* from the Gold Ace Limestone member of the Carrara

Formation, eastern California, *Gogia lockeri* from the Pyramid Shale member of the Carrara Formation, eastern California, and *Gogia mccollumi* from the Saline Valley Formation of western Nevada.

4. The genus attached to skeletal debris or to matgrounds by means of a suction pad at the tip of the holdfast. These are similar in function and morphology to those in the helicoplacoids, and *Camptostroma roddyi* Ruedemann, 1933.

5. *Gogia* grew by addition of new plates at four zones. The boundary between the aboral pad and holdfast served as a zone of plate insertion for the stalk; the boundary between the imperforate extraxial region and perforate extraxial region served as a zone of plate insertion for the perforate extraxial region; the ambulacra grew by addition of plates at the ambulacral tips, and brachioles similarly grew by addition of plates at the tips of the brachioles.

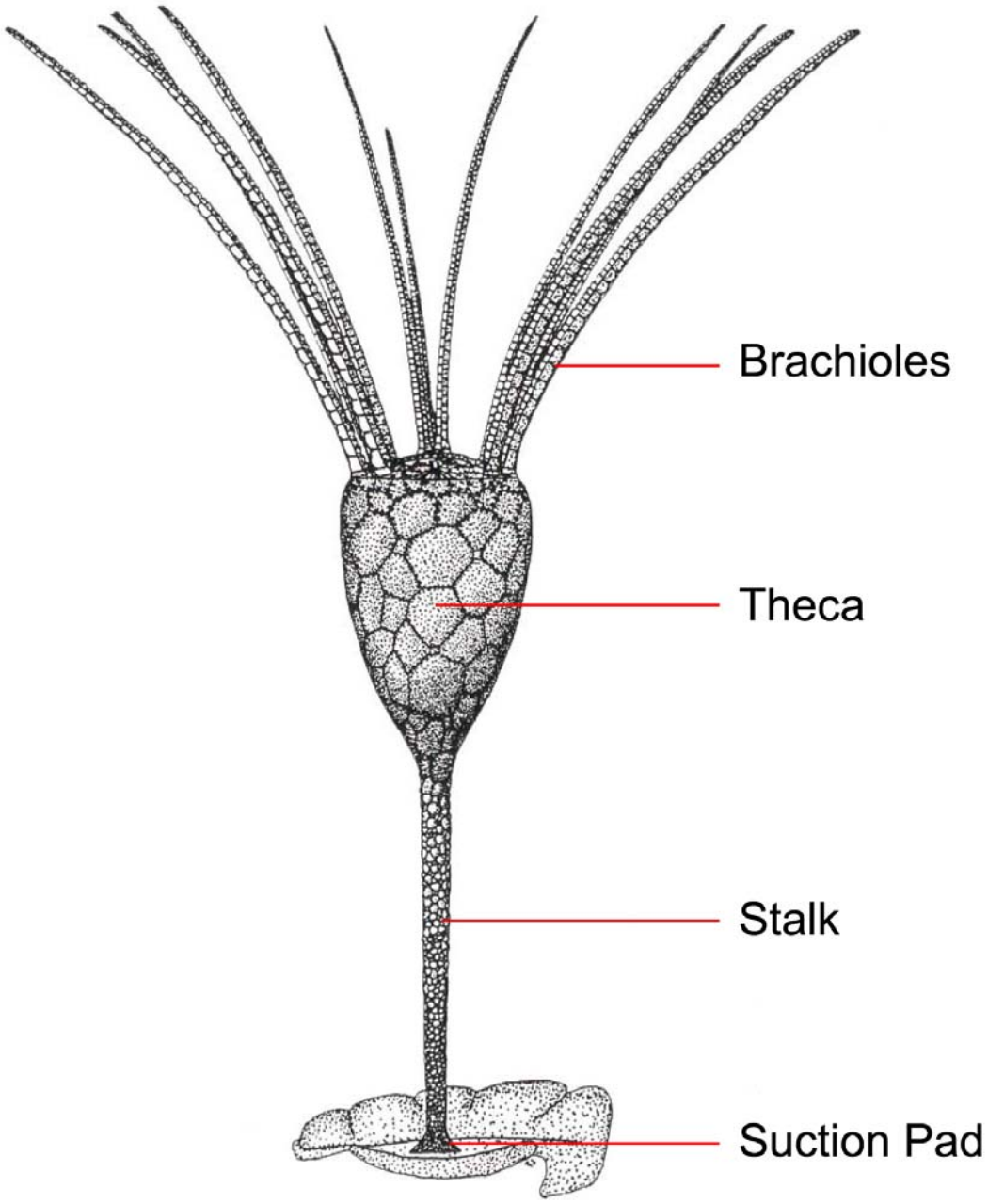


Figure 4.1. *Gogia* reconstruction carried out by Sumrall (1996), based on an undescribed specimen from the Middle Cambrian of Utah.

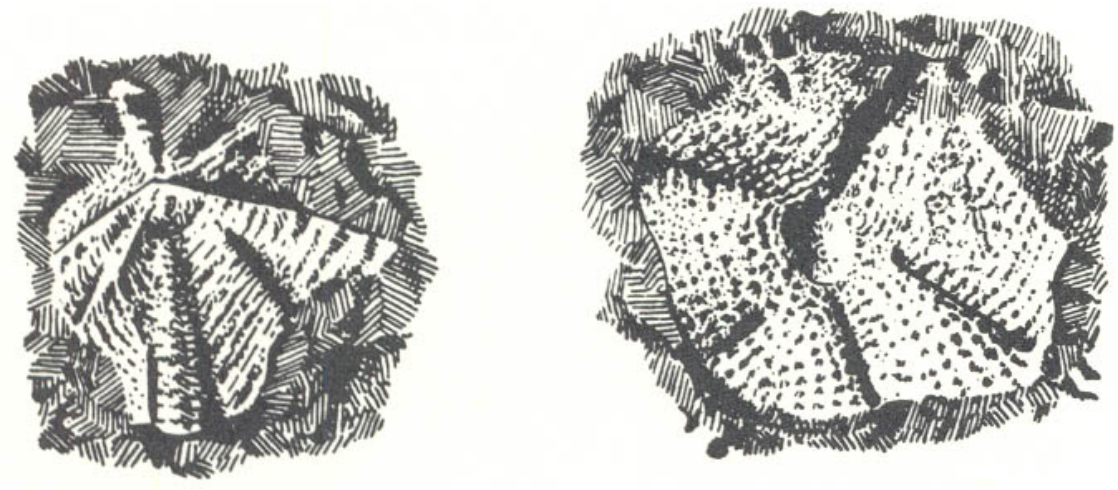


Figure 4.2. *Eocystites primaevus* Billings, 1868. Each plate is 5 mm across. The complete animal, from the Lower Cambrian St. John Group, Nova Scotia, Canada, has yet to be found. Figures from Ubaghs, 1967 (Figure 323, pg. S492).

Figure 4.3. *"Eocystites" longidactylus* Walcott, 1886, later renamed *Gogia longidactylus* by Sprinkle, 1973. Specimen is a lectotype. From the Middle Cambrian Chisholm Shale, southeastern Nevada. Specimen is 41 mm in width; figure is from Sprinkle, 1973 (Plate 10, figure 1).

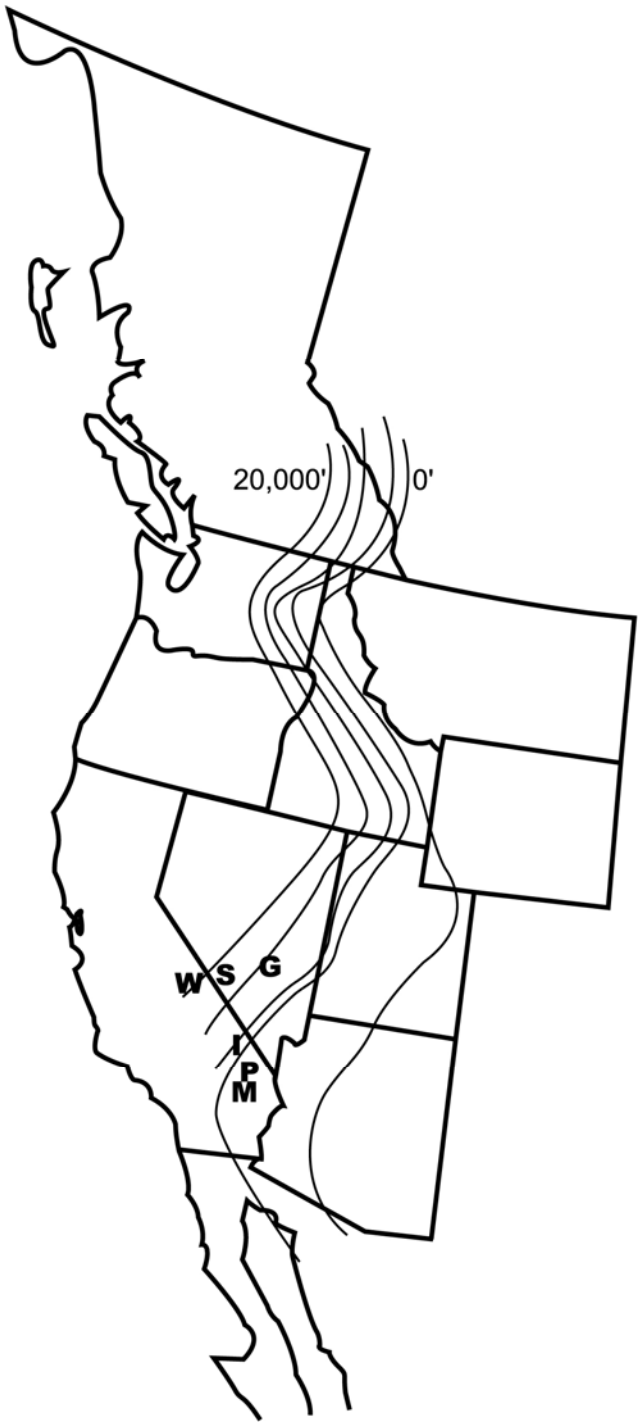
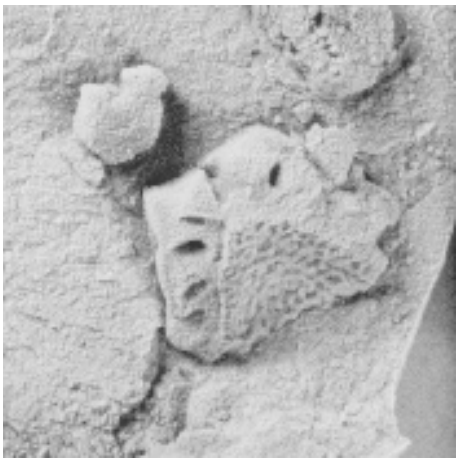


Figure 4.4. Early Cambrian *Gogia* localities. Isopach contours are 5,000’ (1515 m) and indicate thickness of Late Proterozoic and Lower Cambrian rocks. G is the Carrara Formation outcrop in the Groom Range; S is the Saline Valley Formation outcrop in Esmeralda County, Nevada; W is the upper member of the Poleta Formation in the Westgard Pass area; I is the Carrara Formation outcrop in the Immigrant Pass area; P is the Latham Shale outcrop in the Providence Mountains; and M is the Latham Shale outcrop in the Marble Mountains.

A. 

B. 

C. 

Figure 4.5. Oral frame plates of an unidentified edrioasteroid from the Lower Poleta Formation of the Westgard Pass area of the White-Inyo Mountains, eastern California. Each plate is approximately 3 mm in width.

Figure 4.6. Lower pole of *Gogia maccollumi n. sp.* The imperforate extraxial plates that comprise this region are smaller toward the tip and larger toward the upper pole, indicating that plates are inserted at the tip, and grow larger toward the summit. This portion of the skeleton is 10 mm in length.

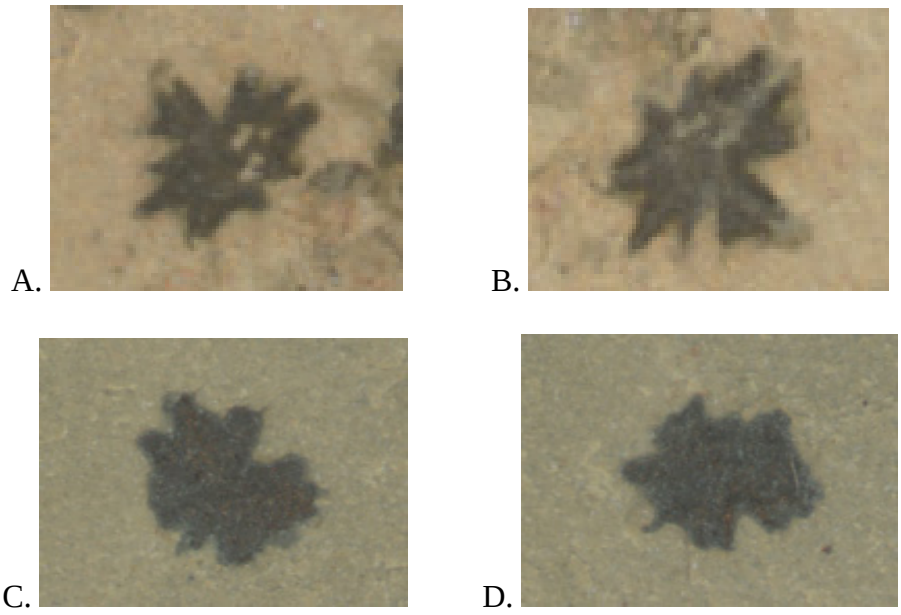


Figure 4.7. Echinoderm skeletal plates from the Montenegro Member of the Campito Formation, Lower Cambrian *Nevadella* zone of eastern California. A and B are part and counterpart pairs, as are C and D. A and B are 3 mm in width, C and D are 4 mm in width. These represent the earliest evidence of skeletized echinoderms in the fossil record.

Figure 4.8. Representative eocrinoid-type plating from siliciclastic beds within the Lower Poleta Formation, White Inyo Mountains, eastern California. Field of view is 20 mm in width.

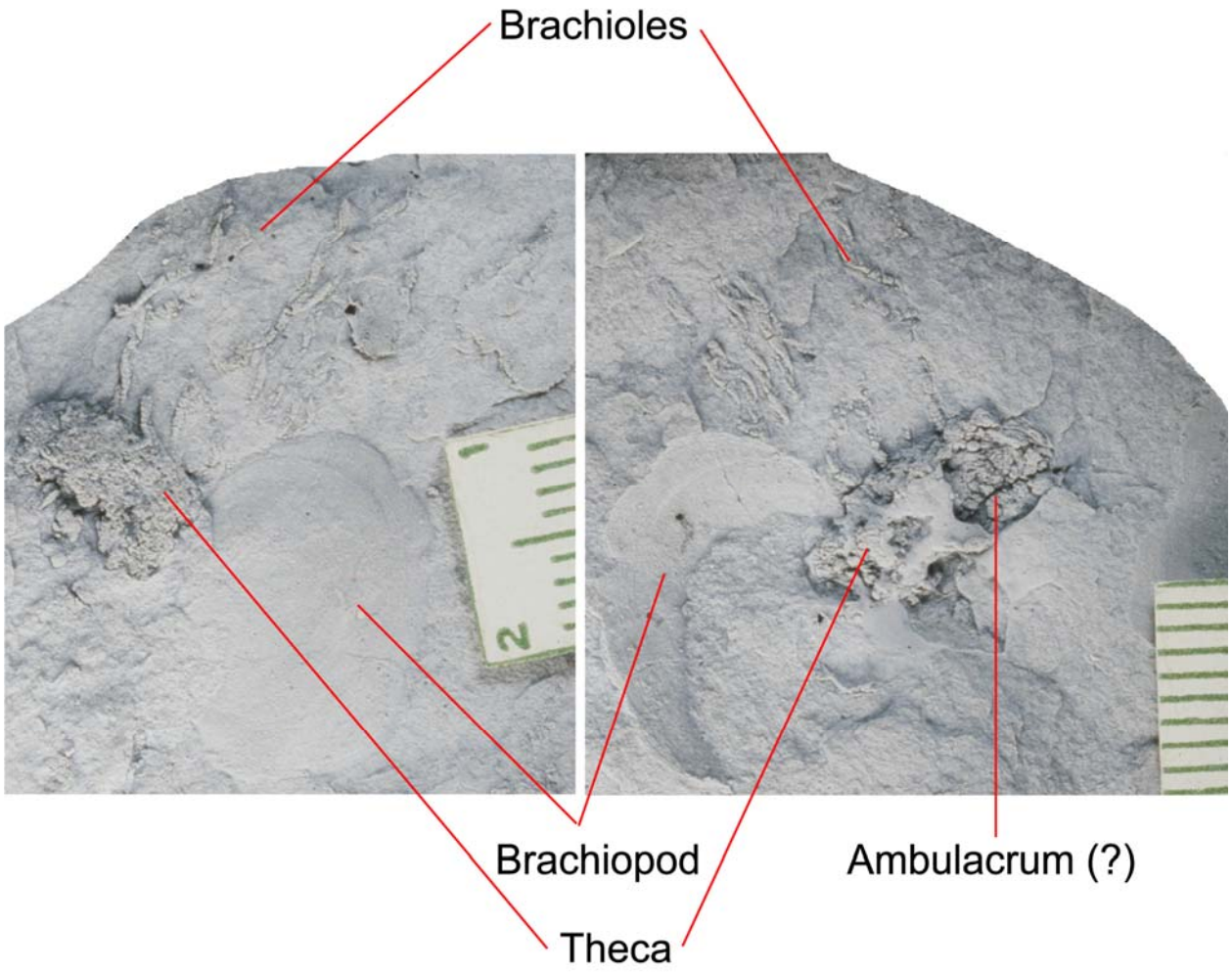
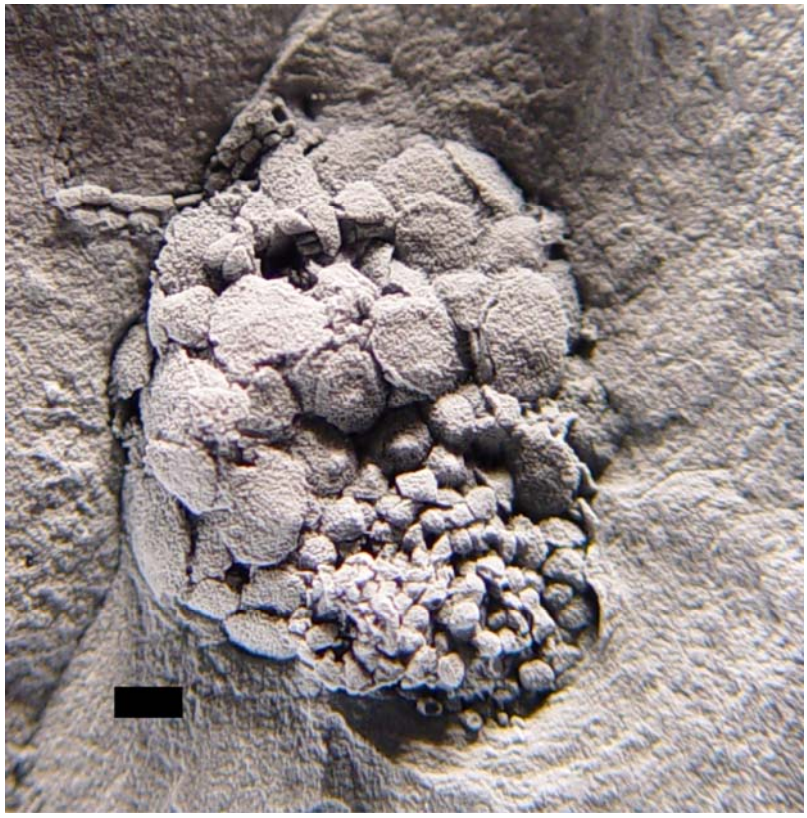


Figure 4.9. Gogia sp. A.,UCMP D-4700, part and counterpart, from the upper member of the Poleta Formation, White Inyo Mountains, eastern California. Specimen shows only portions of the upper theca, a possible ambulacrum, and surprisingly well-preserved brachioles. A portion of metric ruler is included as a scale.

Figure 4.10. *Gogia ojenai* Durham, 1978. Photo is of a cast of UCMP 14526 in part and counterpart. A portion of metric ruler is included as a scale.

Figure 4.1. Proximal portion of two brachioles of *Gogia ojenai*. Brachiole on the left shows uniserial plating. Detail from cast of UCMP 14526; field of view is 3 mm in height.

A.



B.

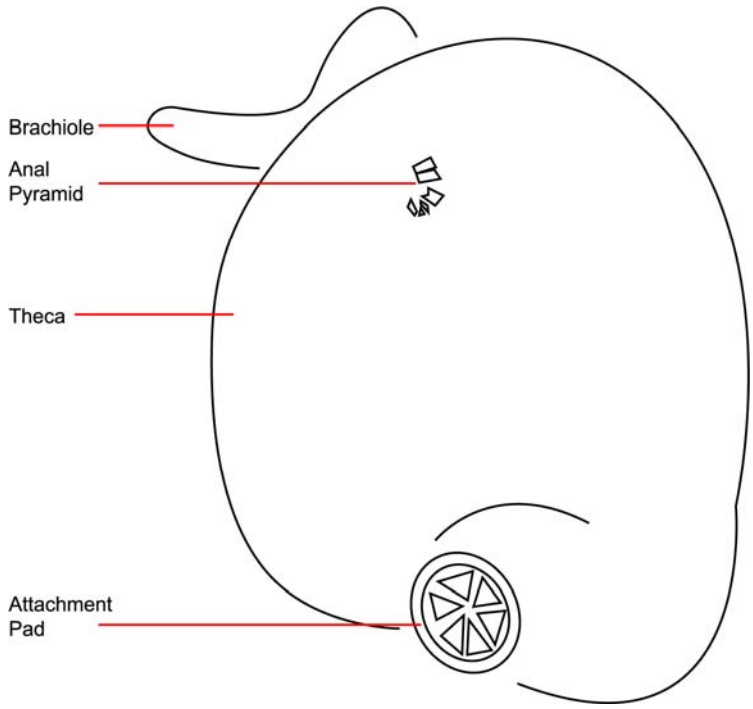


Figure 4.12. *Gogia fowleri n. sp.* A shows a photograph of the specimen, and B shows an interpretive drawing, with morphological features labeled. The scale bar in A is 1 mm long. Specimen is numbered UT TMM 2047TX1a.

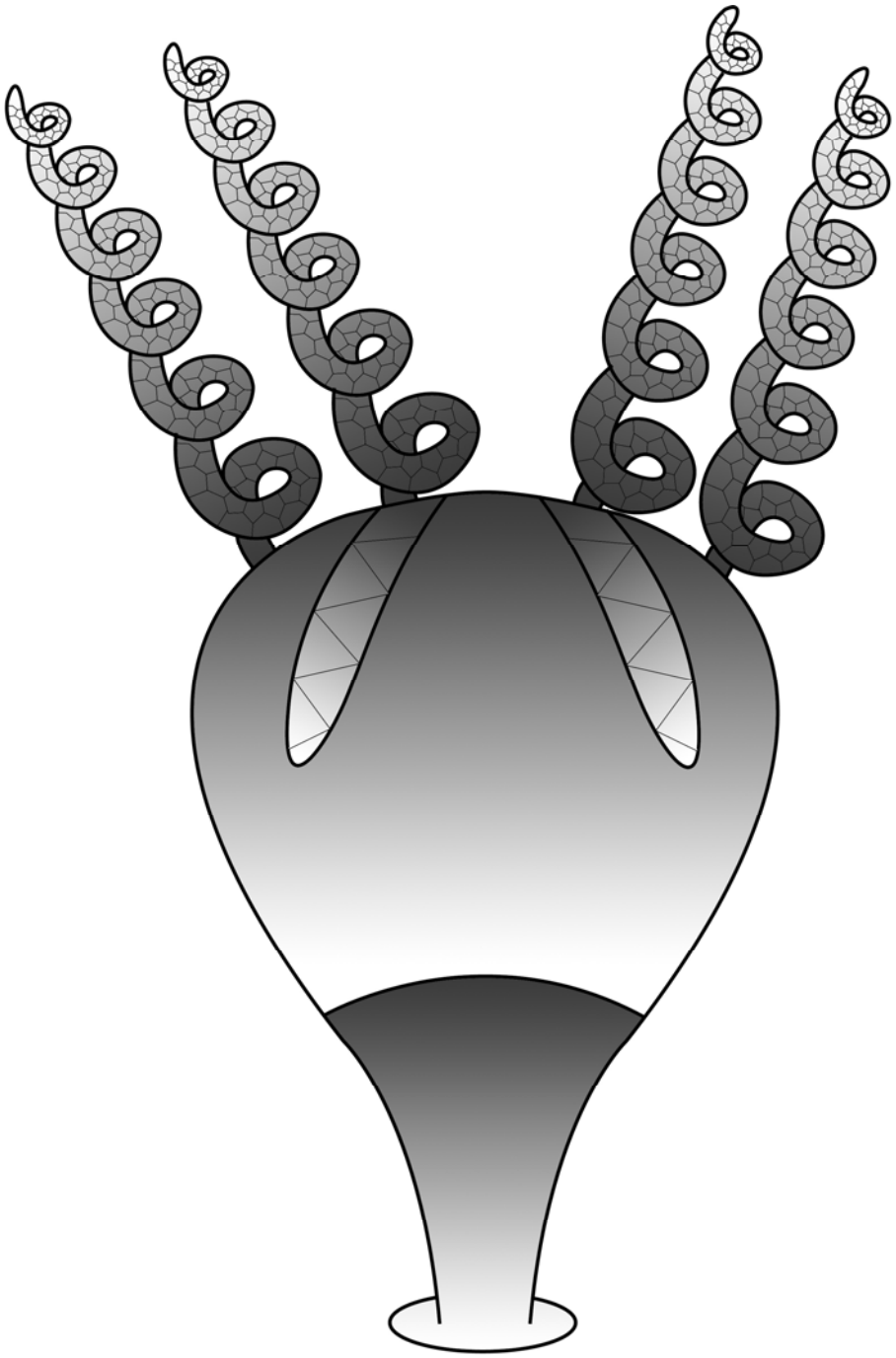


Figure 4.13. Schematic of growth in a generalized *Gogia*. There are four zones of growth, one each for the skeletal regions as designated in the EAT theory. The imperforate extraxial region (IER) grows by plate insertion near the tips; the perforate extraxial region (PER) grows by plate addition at the boundary with the imperforate extraxial region; the axial region (AR, ambulacra and brachioles) grew by plate insertion at the tips. In all zones, the lighter shades indicate younger plates, and darker regions indicate older plates.

Figure 4.14. *Gogia inyoensis n. sp.*, UT TMM 2043TX1a, holotype. Spiraled brachioles stretch from the top of the summit to the left; the holdfast lies to the lower right. Theca is crushed. Note the large epispire bearing plates that comprise the theca in this specimen. A portion of metric ruler is included as a scale.

Figure 4.15. *Gogia inyoensis n. sp.*, UT TMM 2043TX1b, holotype. Upper portion of theca. Note variability in tightness of coiling, especially in the brachiole spiraling off at 1:30 versus the brachioles at 12:00. A portion of metric ruler is included as a scale.

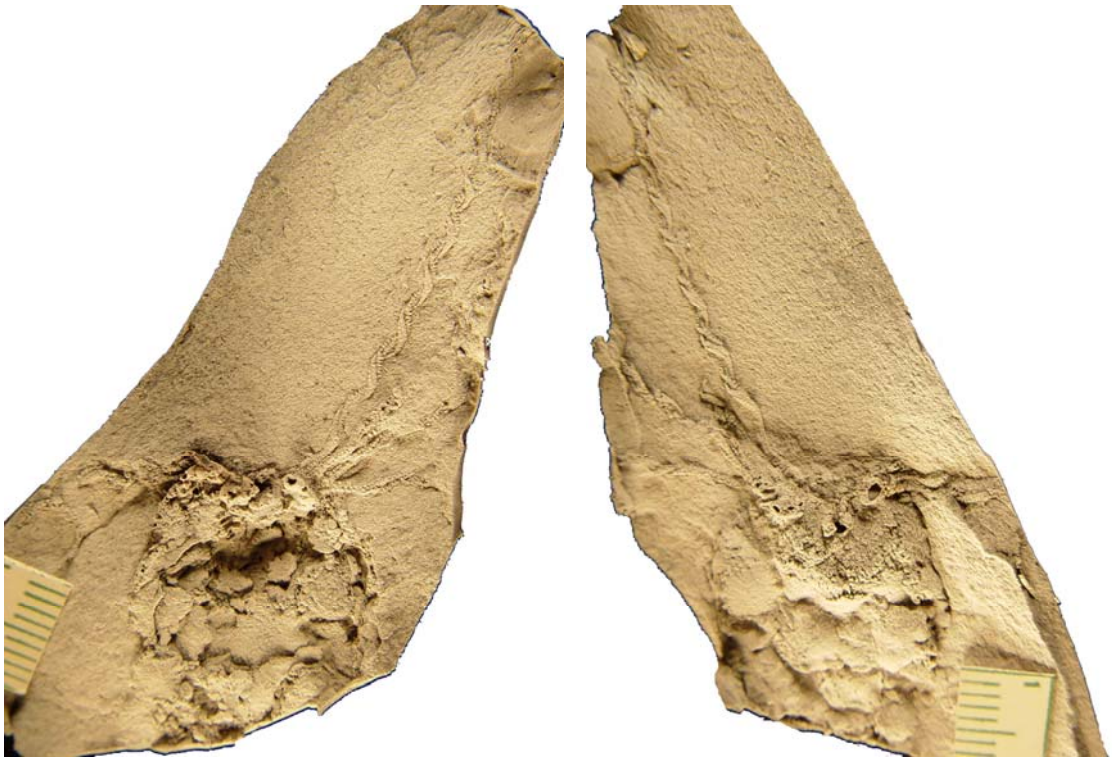


Figure 4.16. *Gogia inyoensis n. sp.*, UT TMM 2044TX1a and b. Both part and counterpart are incomplete but the specimen on the left shows a portion of the holdfast at the base of the theca. Ambulacra show on the summit of the specimen on the right. A portion of metric ruler is included as a scale.

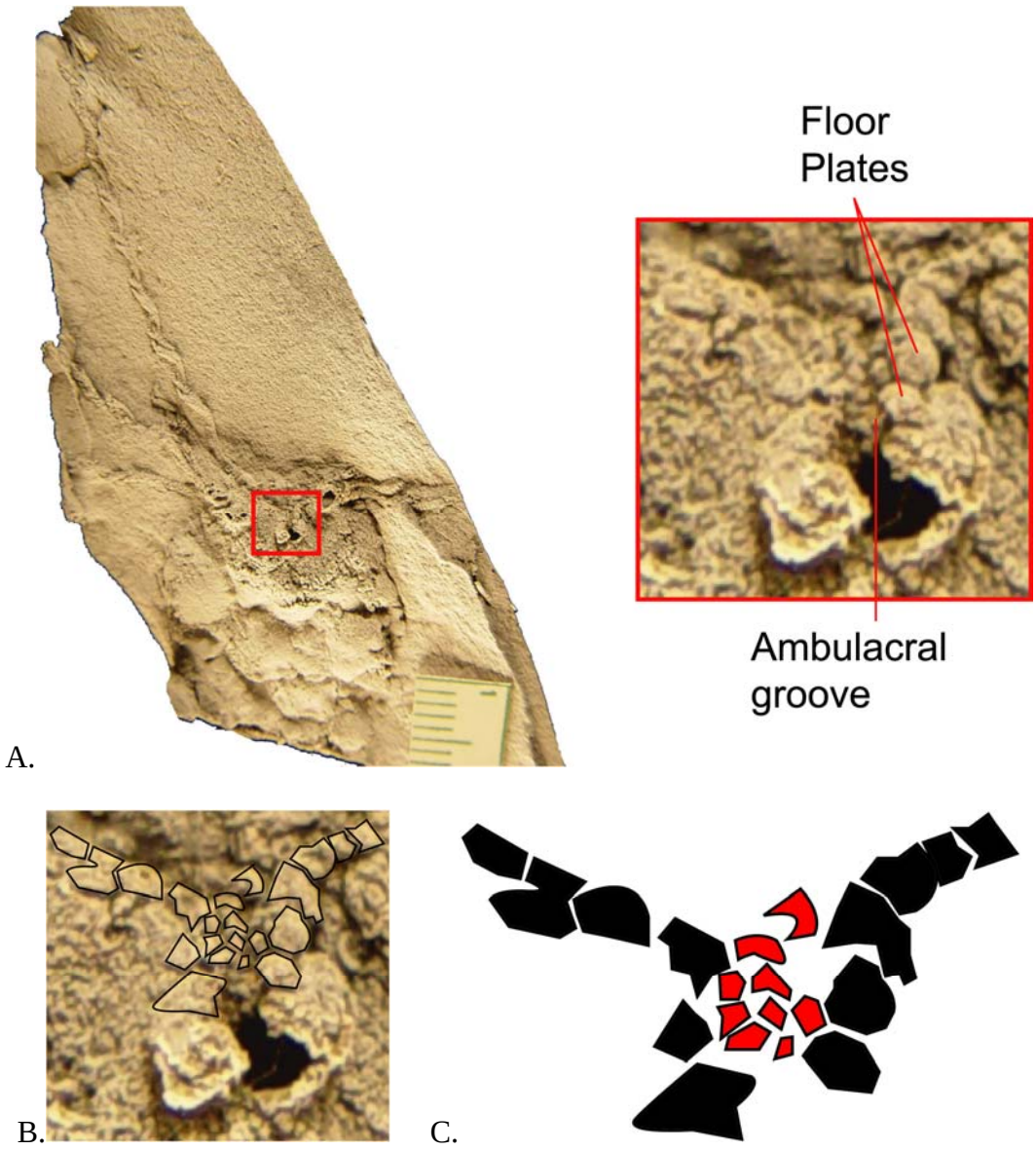


Figure 4.17. Ambulacral groove of *Gogia inyoensis*. B. shows a tracing of ambulacral elements on the enlarged photograph, while C shows assignments of those elements as floor (black) or cover (red) plates. A portion of metric ruler is included as a scale in the photograph.

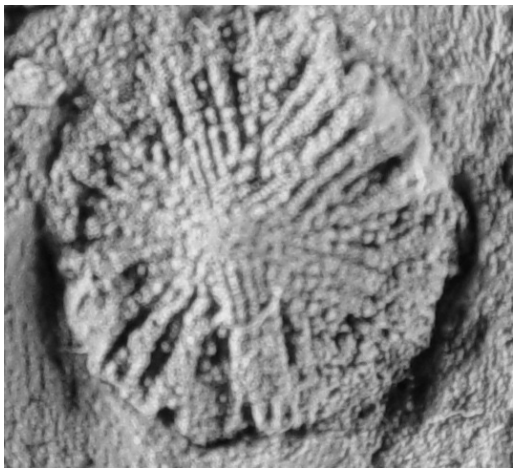
A.  B. 

Figure 4.18. Isolated plate elements from *Gogia inyoensis*. A (UT TMM 2043TX2) shows the exterior, and is 6 mm in diameter. B (UT TMM 2043TX3) shows the interior, and is 7 mm across.

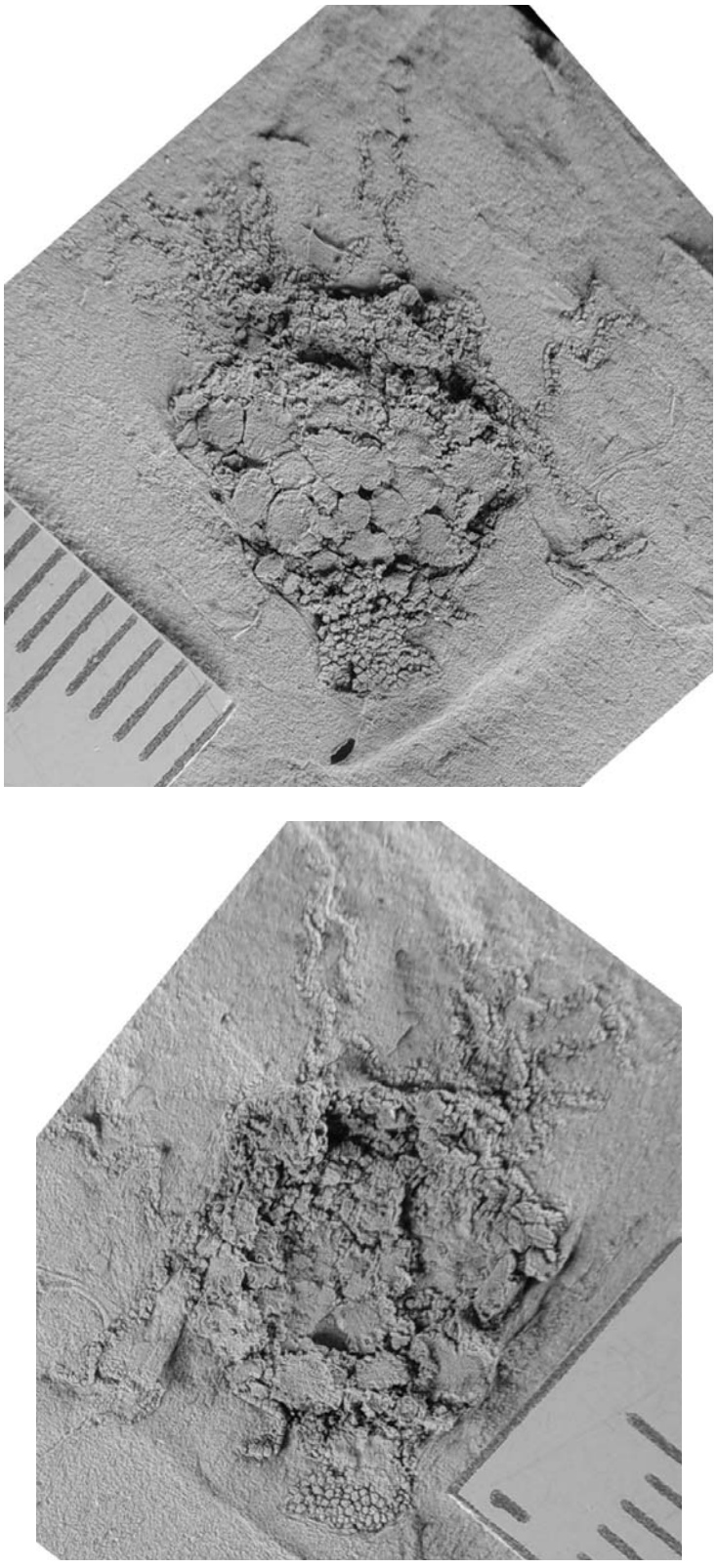


Figure 4.19. *Gogia lockeri n. sp.*, UT TMM 2045TX1a and b, holotype. A portion of metric ruler is included as a scale.

Figure 4.20. *Gogia lockeri n. sp.*, UT TMM 2045TX2. The specimen is pyritized and is therefore obscured, but nonetheless shows the diagnostic lack of ornament on plates. Field of view is 12 mm in height.

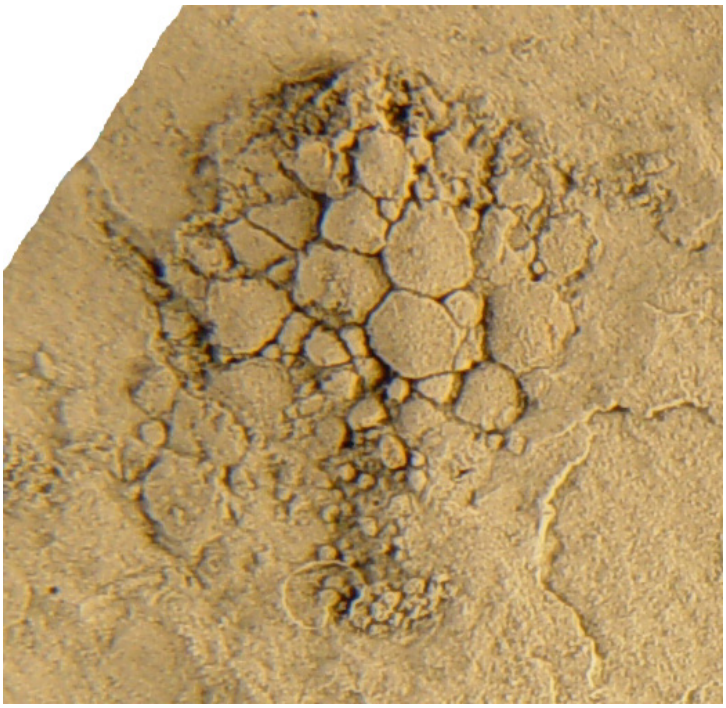


Figure 4.21. *Gogia lockeri n. sp.*, UT TMM 2045TX2. This specimen is on same rock as the specimen in figure 20. This *Gogia* is 8 mm in height.

Figure 4.22. *Gogia lockeri n. sp.,* UT TMM 2045TX3. Summit and brachioles of an incomplete specimen. Note variable coiling of the brachioles. A portion of a metric ruler is included as a scale.

Figure 4.23. *Gogia lockeri n. sp.*, UT TMM 2045TX4. This specimen is poorly preserved, but shows the theca pressed upon the cephalon of an Olenellid trilobite, which suggests the skeletal fragment may have been a substrate used for attachment. Field of view is 23 mm in height.

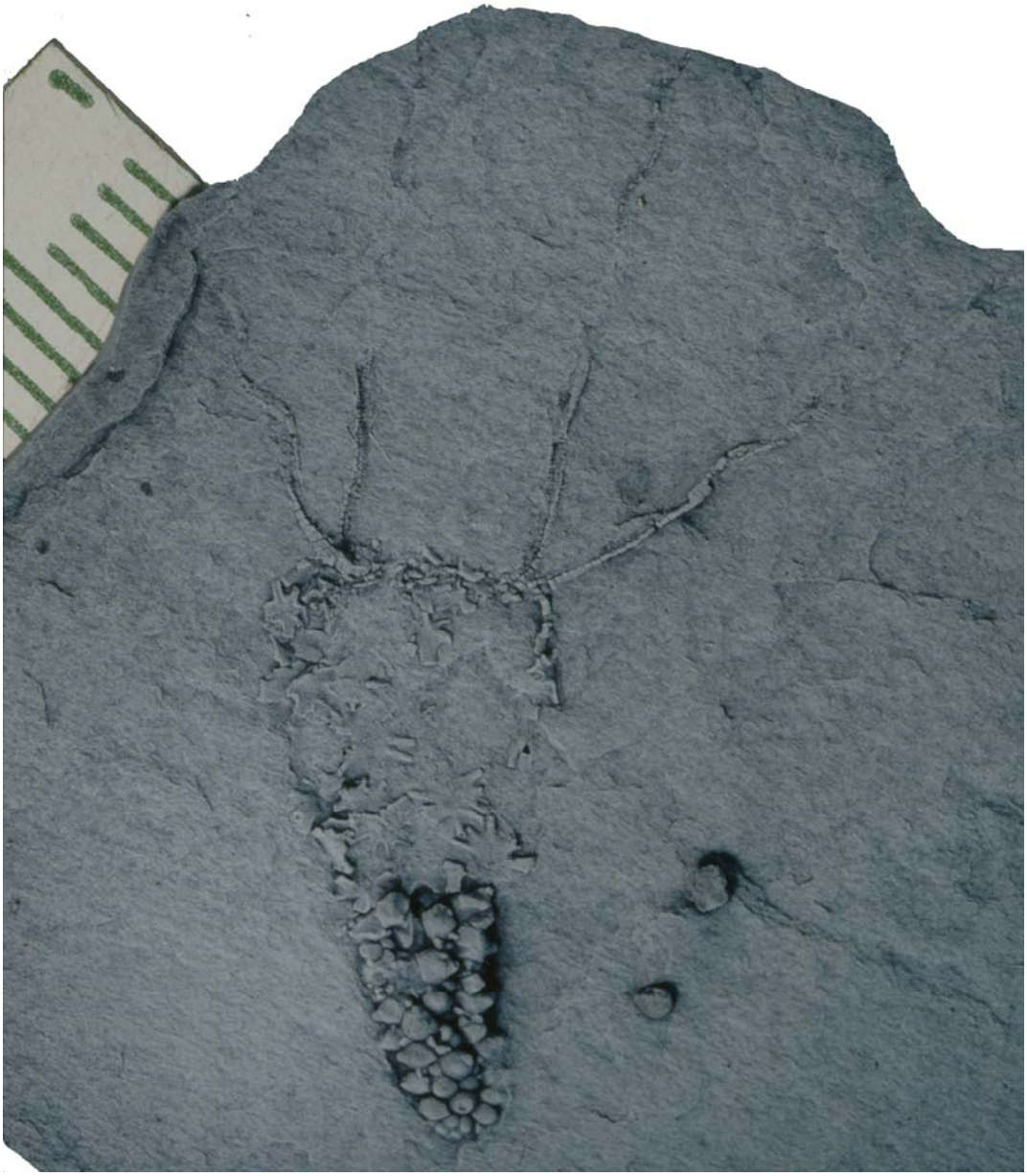


Figure 4.24. *Gogia maccollumi n. sp.*, UT TMM 2046TX1. Metric ruler is included as a scale.

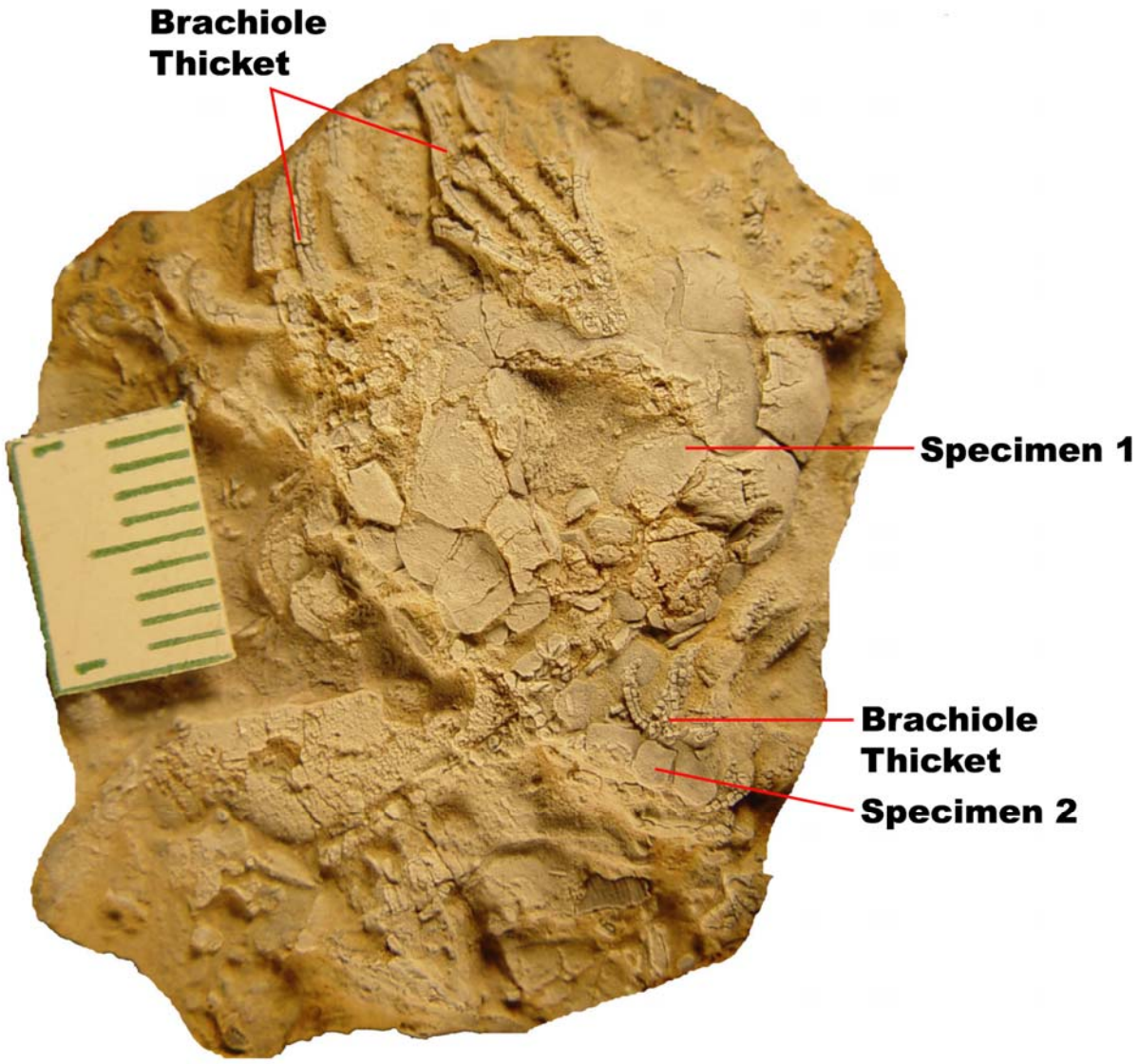


Figure 4.25. Gogia sp. B, UT TMM 2049TX1. Metric ruler is included as a scale.

Chapter 5 – *Schuchertidiscus walcotti* Schuchert, 1919

Introduction

Schuchertidiscus walcotti Schuchert, 1919 is an edrioasteroid echinoderm from the Lower Cambrian *Bonnia-Olenellus* zone of Bonne Bay, Newfoundland, Canada (Figure 5.1). The animal is discoidal in outline, with the oral surface facing upward in life, and the aboral surface resting upon the sediment-water interface. Five straight ambulacra radiate in a "2-1-2" pattern (Sprinkle, 1973) from the mouth, which is located at the center of the oral surface. Five wide triangular interambulacral areas situated between ambulacra are composed of epispire-bearing plates, with an anal pyramid at the distal edge of the CD interray. The oral surface meets the aboral surface at a peripheral rim, which is oriented downward toward the sediment-water interface. The aboral surface is composed of tightly sutured plates without epispires, and a "centrodorsal" dodecahedral plate in the middle of the aboral surface (Schuchert, 1919).

The fossil was discovered by Charles Schuchert in 1910, and described by him in 1919. Schuchert placed it in the Genus *Stromatocystites* Pompeckj, 1896 (Figure 5.2), a genus erected to house a species of edrioasteroid from the Middle Cambrian Jince Formation of the Příbram-Jince beds of Bohemia, Czech Republic (Havlíček, 1998; Parsley and Prokop, 2001, 2004). Schuchert (1919) wrote that the overall similarity was great enough that the new species belonged in the established genus. However, the animal shows enough disparity in the aboral region that it clearly does not belong in genus *Stromatocystites*, especially considering the stratigraphic distance, geographic distance, and temporal distance between the taxa. The stratigraphic interval over which

this fossil is found matches that of *Camptostroma roddyi*, with which it shares the distinction of being the first edrioasteroids in the geologic record, and among the oldest echinoderms.

Past Work and Occurrences

The genus *Stromatocystites* was erected by Pompeckj (1896) to house a new edrioasteroid from the Middle Cambrian Jince Formation of the Příbram-Jince beds of Bohemia, Czech Republic (Figure 5.2). The taxon, *Stromatocystites pentangularis*, is found within 150 m of gray-green greywackes with interbedded quartzose sandstone and quartz-pebble conglomerate, known initially as the "*Stromatocystites* Zone" (Šuf, 1928; Havlíček, 1998). Subsequent biozonation has focused on trilobites, resulting in the new designation "*Hydrocephalus minor* Zone" (Havlíček, 1998). An epicontinental sea transgressed the basin during the Middle Cambrian, resulting in the deposition of these sedimentary rocks.

The fossils also occur in the lower portion of a 20 m thick section of gray-green shales and sandstones within the "*Paradoxides gracilis* Zone," named for the abrupt first appearance of the index fossil (Havlíček, 1998). The temporally equivalent Skryje shales crop out approximately 30 km to the northwest of Jince. These rocks also contain the remains of S*tromatocystites*. Aside from the aforementioned trilobite index fossils, the edrioasteroid occurs with the eocrinoids *Acanthocystites briareus* Barrande, 1887 (Ubaghs, 1968b), *Lichenoides priscius* Barrande, 1846, *Lichenoides vadosus* Parsley and Prokop 2004, and the enigmatic echinoderm *Cigara dusli* Barrande, 1887 (Ubaghs, 1968b; Sprinkle, 1973; Parsley and Prokop, 2004)

The original description of the genus is as follows (from the translated description related by Schuchert, 1919): Flat cystid; pentagonal unstalked thecal made of as many as 1,000 large non-imbricate pentagonal and hexagonal plates bearing "diplopore" depressions. Oral surface convex, lower surface concave; aboral surface plates finely pitted; ambulacra restricted to the oral surface; ambulacra are composed of 11 to 13 elongate biserial plates and the same number of covering plates; mouth surrounded by four large and several small imperforate plates; anus covered by a pyramid of plates in the "bivium on the upper side" (CD interray) (Pompeckj, 1896; Schuchert, 1919). At the time of publication, the genus was monotypic (Pompeckj, 1896).

The new species *Stromatocystites balticus* Jaekel, 1899 was described from a glacial erratic block from the Middle Cambrian *Paradoxides paradoxissimus* Zone, Germany. The description given in Jaekel (1899) was argued by Smith to be too general to distinguish this species from *Stromatocystites reduncus*. Furthermore, the original specimen has since been lost, further justifying treatment of the name as a *nomen dubium* (Smith, 1984)

Bather (1900) discussed *Stromatocystites* in his taxonomic revision of the Edrioasteroidea included in the echinoderm volume in the Treatise on Zoology. He considered *Stromatocystites* "primitive," and close to what could be considered a hypothetical ancestral echinoderm. It was placed in Family Agelacrinidae, which was originally named Agelacrinitidae (Chapman, 1960), but as was habit by Bather, arbitrarily renamed. Furthermore, Bather renamed the genus "*Stromatocystis*," which is similar to the treatment given the Middle Cambrian eocrinoid *Eocystites*, which was renamed "*Eocystis*" (see chapter herein on *Gogia*.) The new observations on

Stromatocystites included that the animal was probably sessile, was fixed to substrates by its lower surface, but not permanently, and interambulacral plates are hexagonal and smaller toward the edge of the oral surface (Bather, 1900). As the name changes proposed by Bather are junior synonyms of the original names, none of them are valid.

A new species *Stromatocystites cannati* Miquel, 1905 was included in the genus. The fossil, from the Middle Cambrian of Montagne Noire, France, was originally named *Trochocystites cannati* Miquel 1894, before being renamed (Miquel, 1905), likely to highlight an inferred similarity to Pompeckj's manuscript describing *Stromatocystites pentangularis*. The ambulacral areas are comparatively large, and the oral surface is bordered by few large rectangular plates, traits that Schuchert (1919) argued excluded the taxon from *Stromatocystites*. These arguments were later borne out in a discussion of the fossil by Cabibel et al. (1958) wherein it was renamed *Cambraster cannati* Miquel 1894 (Cabibel et al., 1958; Termier and Termier, 1969).

Charles Schuchert added the new taxon *Stromatocystites walcotti* Schuchert, 1919 to the genus in a short paper preceding a larger tome on the stratigraphy of western Newfoundland, Canada (Schuchert and Dunbar, 1934). These are the fossils discussed herein. The fossils are found in an unnamed formation accounting for 673 m (2,208 feet) of Lower Cambrian rock at Bonne Bay. "Bed 25," 9 m (30 feet) thick and 182 m (597 feet) from the top of the section, and "Bed 1," 12 m (40 feet) thick and 146 m (480 feet) from the base of the section yield edrioasteroid fossils and the index trilobite *Olenellus thompsoni* (Schuchert and Dunbar, 1934). "Bed 25" is composed of dark shales and interbedded sandstones, and "Bed 1" is composed of limy shales and interbedded quartzites; approximately 345 m (1,131 feet) of section separate these beds. No

indication is given in the literature or with the type specimens to indicate which of these beds the type specimens were collected; the great distance between them suggests the possibility of two different species, but no clear delineation can be made based on study the study of the paucity of material currently available. Schuchert did note that those specimens collected fall into two size bins; one small and the other large. Fossils of each different size occur at two different intervals, designated *Stromatocystites walcotti* (Figure 5.3), and *Stromatocystites walcotti minor* (Figure 5.4) (Schuchert, 1919).

Schuchert (1919) did not write a standard diagnosis of *Stromatocystites walcotti*; he chose instead to reprint a translated diagnosis of *Stromatocystites pentangularis*. It can be assumed that Schuchert decided on delineating *S.* walcotti as a separate species based on discussion of a few diagnostic characters, despite not mentioning these as such. The central aboral area is composed of a "centrodorsal plate" with 10 surrounding pentagonal plates. There are also apparently fewer plates upon the oral surface; *S. walcotti* was described as having 120 to 130 plates, while *Stromatocystites pentangularis* was described by Pompeckj (1896) as having 1,000 plates. The former also varies in stratigraphic position, occurring in the Lower Cambrian (Schuchert, 1919).

Schuchert agreed with Bather that the animals were impermanently attached, and ventured to hypothesize that this along with the environment of deposition fostered the adaptive landscape for the development of the asteroids. The depositional environment (shales and sandstones) was inferred to receive a tremendous influx of sediment in a high energy nearshore regime, which could have buried the fossils or flipped them over, requiring tube feet that were large enough to excavate the surface or right it. Once this ability was adapted, the ability to "creep" around on the sea floor on ambulatory tube feet

followed, permanently altering the evolutionary trajectory of the group (Schuchert, 1919).

Bassler (1935, 1936) included *Stromatocystites* in a pair of papers on edrioasteroid classification. The first included the genus in the new family Agelacrinitidae Bassler, 1935, and erroneously referred to it by the junior synonym *Stromatocystis* Bather, 1900 (Bassler, 1935). The next paper (Bassler, 1936) moved the group to the new family Stromatocystitidae Bassler, 1936, and properly referred to the taxon as *Stromatocystites* Pompeckj, 1896.

Cabibel at al. (1958) wrote a short paper on the Middle Cambrian echinoderms of the Montagne Noire region of southern France. The authors, as already mentioned, reassigned *Stromatocystites cannati* to the new genus *Cambraster*, and illustrated a reasonable reconstruction of *Stromatocystites pentangularis*, including the aboral surface. It shows a pentagonal area bordered by a ridge that extends to the edge of the aboral surface, which is drastically different from the centrodorsal plate of *Stromatocystites walcotti*. The authors also tentatively assigned a new poorly preserved echinoderm from the Middle Cambrian of southern France the name *Stromatocystites ?* sp. (Cabibel et al., 1958).

Termier and Termier (1969) were the first to reconstruct the theca of *Stromatocystites walcotti*, and concluded that at the terminus of each ambulacrum lay an inhalant orifice used for respiration (Figure 5.5). This premise would require fused coverplates, and would leave the animal without a means of feeding, save for sieving incoming water, a feeding mode not seen in any early echinoderms. The order Stromatocystitoida Termier and Termier, 1969 was erected to further delineate these

echinoderms from other edrioasteroids. Termier and Termier suggested that the size disparity in the species was a result of ontogenetic variation rather than taxonomic, which negates the necessity of Schuchert's (1919) sub-specific assignment of the smaller ontogenetic stage as "*minor*." (Termier and Termier, 1969).

Paul and Smith (1984) reviewed the anatomy of *Stromatocystites walcotti* in a review on the radiation and phylogeny of early echinoderms. The authors discounted the idea of terminal ambulacral orifices advanced by Termier and Termier (1969), suggesting that structures misinterpreted as orifices are merely weathered edges of the theca, exposing the food groove. As stated in previous work, the oral surface is composed of epispire-bearing plates, which are larger at the edge of the theca. It was presumed to have been a low-level suspension feeder with no means of attachment to the substrate surface, which was considered adaptive in higher energy environments that could potentially dislodge and wash away an animal with more relief. At the marginal ring is a zone of smaller imbricate plates, presumed to represent a growth zone. Included with two figures of *Stromatocystites walcotti* was a reconstruction of the ambulacra of *Stromatocystites pentangularis* (Paul and Smith, 1984).

Jell and Smith (1990) described a new species of edrioasteroid from the early Middle Cambrian *Redlichia* zone of the Yelvertoft Member, Beetle Creek Formation, 45 kilometers west-southwest of Mount Isa, Queensland, Australia. The echinoderms occur in a laminated chert, which is interbedded with a silicified coquinite, algal chert, and siltstones.

The fossils, first discussed in Jell et al. (1985) before further collection warranted a description, are highly suggestive of the taxon *Stromatocystites pentangularis*,

especially in the medial aboral region. Both taxa have a pentagonal medial pad with a raised rim, and radiating linear ridges leading away from each vertex of the central pad, opposite the ambulacral areas upon the oral surface (Figure 5.6). The interiors of these structures in both *Stromatocystites pentangularis* and the new species show myriad radial struts leading away from the interior of the central pad, leading the authors to suggest that these were radial muscular attachment sites similar to those found in *Totiglobus nimius* (Bell and Sprinkle, 1978). By contracting the radial musculature, the authors reasoned, the pad would be puckered, initiating a seal against a hard substrate (Smith and Jell, 1990).

Because of this synapomorphy, the new fossil was named *Stromatocystites reduncus* Smith and Jell, 1990. The specific epithet was designated in reference to the diagnostic curved ambulacra unique to this group. However, the particular characters used to diagnose the new species as belonging to *Stromatocystites* are not found in *Stromatocystites walcotti*, which has an aboral "centrodorsal" plate rather than a raised pentagonal pad, suggesting a different means of attachment, and possibly a new taxonomic affinity.

Guensburg and Sprinkle (1994) conducted a phylogenetic analysis of early edrioasteroids, wherein they considered *Stromatocystites walcotti* sufficiently disparate to refer to it as "*S.*" *walcotti*, a reference justified by the paraphyly of Stromatocystitidae confirmed by the phylogenetic analysis. The authors further suggested that the taxon represents a new genus, but declined redescribing and renaming it considering the focus of the paper was systematic and not descriptive (Guensburg and Sprinkle, 1994).

A final species, *Stromatocystites flexibilis* Parsley and Prokop, 2004 was added to the genus, but the publication date for the new species is well past the point it was established that *Stromatocystites walcotti* belongs in a different group than its Bohemian counterparts, and so will therefore not be discussed here (Parsley and Prokop, 2004).

Material Studied

Stromatocystites walcotti is known primarily from two specimens from the United States National Museum, the holotype, USNM 66443 and USNM 376690. Both are preserved aboral-side up, and both lack counterparts. What little is known of the oral surface is known from the holotype, which has a damaged aboral surface that exposes the interior of the oral surface in parts of three interambulacra. The other specimen has a taphonomically removed lower surface, and shows the complete internal view of the oral surface, which shows an exceedingly well-preserved ambulacral floorplate series, but nearly no detail in the interambulacral areas. Three additional juvenile (*Stromatocystites walcotti minor*) specimens were studied, but show so little detail they lack value for systematic studies. These specimens, USNM 384979, USNM 384980, and USNM 384982, were originally designates *Stromatocystites walcotti minor* by Schuchert (1919). All that has been written regarding the oral surface and ambulacral coverplates of *Stromatocystites walcotti* has been based on those of *Stromatocystites pentangularis* (Schuchert, 1919; Paul and Smith, 1984.)

Morphology

The system of skeletal homology recognized by Mooi and David (1997, 1998) provides a framework for discussing the morphology of *Stromatocystites*, along with other early echinoderms. The Extraxial-Axial Theory (EAT) draws comparisons of developmental and functional regions across the spectrum of the echinoderm bauplan to characterize homology. The skeleton is delineated into three separate skeletal regions, the axial, perforate extraxial, and imperforate extraxial. The axial region is the portion of the skeleton dedicated to support of the hydrovascular system. The perforate extraxial region is involved in coelom enclosure, and is "perforated" by sutural pores, which likely allowed for respiration. The imperforate extraxial region is dedicated to coelom enclosure, but lacks respiratory openings. In modern crinoids and in many early groups (Mooi and David, 1997, 1998; Peterson et al., 2000) this skeletal region is dedicated to holdfast structures, or to other substrate attachment.

Axial Region

The axial region in *Stromatocystites* is expressed as five straight ambulacra arranged in a "2-1-2" pattern about the mouth, and unequivocally the best-preserved oral frame of any Cambrian echinoderm. However, because of the preservation of the two adult specimens, the ambulacral coverplates are unknown. The oral frame (Figure 5.7) is composed of a ring of 11 plates; two "primordial ambulacral plates" form the base of each ambulacrum, and a long "hydropore plate" (Paul and Smith, 1984) bridges the gap between the primordial ambulacral plates of the C and D ambulacrum (Carpenter, 1884). No hydropore has been observed in any specimens, but considering the placement of this

orifice in other edrioasteroids and the irregularly large size and position of this plate in *S. walcotti*, it is likely that this plate has some relation to the hydropore.

Ambulacral plates are biserially arranged, with a distinctive zigzag suture along the floor of the ambulacrum (Figure 5.8). Plates proximal to the mouth are larger than distal plates, suggesting plate insertion at the mouth. More mature plates have a structure different than that of other Early Cambrian echinoderms. Away from the midline of the ambulacrum, the floorplates have two long finger-like projections that interdigitate with adjacent interambulacral areas. Between plates these projections make space available for the ampullae of the overlying radial water vessel. The projections were attachment processes for ligaments or musculature that connected the oral surface to the aboral surface. A discussion of the purpose and function of these ligaments follows in the section on Paleoecology.

Hotchkiss (1998) used the oral frame of *Stromatocystites walcotti* as the model for his "Rays as appendages" model of the origin of pentamery in echinoderms. His model stemmed from the observation that ambulacra A, C, and E have the right primordial ambulacral plate (viewed from above the oral surface) proximal to the mouth, while B and D have the left primordial ambulacral plate proximal to the mouth. This led to the supposition that ambulacra B and C were duplicated to from ambulacra D and E from an original triradiate condition. This is unlikely, as the original echinodermal condition subscribed to herein is a "2-1-2" pattern (see discussion of helicoplacoid ancestry). It is possible the arrangement is due to spatial problems associated with the elongate hydropore plate, and 2-1-2 ambulacral morphology.

Perforate Extraxial: Thecal surface, epispires

The perforate extraxial region of *Stromatocystites walcotti* is preserved only in internal view at the distal-most edges of the CD and DE interrays in specimen USNM 376690, portions of three interrays of specimen USNM66443, and upon juvenile specimens, which are not mature enough to show emergent traits. The interrays are composed of large polygonal plates with epispires arranged along the edges. There is no evidence of epispire covers or an inferior layer of plates as in *Camptostroma.* The external surface of the interrays is known only from the juvenile specimens, which show irregular linear series of pustules upon the surfaces (Figure 5.9), similar to ornament on the surfaces of some species of *Gogia* and *Camptostroma*, but none in any repeating predictable patterns.

The anal pyramid is clearly visible in internal view at the edge of the CD interray of specimen USNM 376690. The structure is fringed by many lath shaped plates that suggest that it was elevated in life. The anal pyramid lies toward the D ambulacrum instead of lying along the midline of the animal. No evidence for the hydropore exists other than the aforementioned elongate hydropore plate bridging the gap between the C and D ambulacra.

The edge of the oral surface abuts a ridge of downward oriented plates forming a peripheral rim with the edge of the imperforate extraxial region. The edges of USNM 66443 show small plates at the very edge of the theca, and larger plates immediately adjacent toward the centrodorsal plate (Figure 5.10). The smaller of these plates are the distal-most edges of the perforate extraxial region, and probably constitute a zone of plate addition.

Imperforate Extraxial

The imperforate extraxial region accounts for the aboral surface of *Stromatocystites*. The aboral portion of the peripheral rim visible in the type specimens shows large plates lacking epispires; USNM 66443, plates get larger toward the center of the aboral surface. The rim stands out in relief, giving the aboral surface a concave profile, originally discussed by Schuchert (Figure 5.11) (1919). The aboral surface consists of a pavement of tightly sutured tessellate plates, with a single large polygonal "centrodorsal plate" at the center. There is no relief aside from the general concavity to the surface, unlike the aboral ridges in *Stromatocystites pentangularis* and *Stromatocystites reduncus* (Termier and Termier, 1969; Smith and Jell, 1990).

Paleoecology

Schuchert (1919), Paul and Smith (1984), and Smith (1985) argued that *Stromatocystites walcotti* was unattached in life. While Bather only briefly mentioned that *Stromatocystites* may have been impermanently attached. The latter conclusions however were based on observations of *Stromatocystites pentangularis* and under the assumption that these were similar taxa. While low in profile, reducing the drag from currents on the theca, these echinoderms were nonetheless attached in life. The lines of evidence for this function come from the anatomical features of the ambulacral plates, aboral surface, and peripheral rim.

Each of the ambulacral floorplates bear a pair of finger-like projections oriented perpendicular to the axis of the ambulacrum (Figure 5.12). These structures are similar to

those seen in the isorophid edrioasteroids *Spiraclavus nacoensis* Sumrall, 1992 (Sumrall, 1992), *Hypsiclavus kinsleyi* Sumrall, 1996, and *Hypsiclavus huntsvillensis* Sumrall, 1996 (Sumrall and Parsley, 2003). These three edrioasteroids are all discocystinids, with a domal oral area, and a telescoping pedunculate zone made of imbricate plates, that elevated the oral area in the water column. Cloacal pumping is responsible for thecal inflation (Farmanfarmaian, 1966; Nichols, 1969; Binyon, 1972; Bell, 1977; Sumrall, 1992), while retraction of the theca was accomplished through opening of the anal pyramid and rapid egress of water by ligamental contraction of the theca. Ligaments were attached on one end to the interior of the aboral surface and to projections of the sides of the ambulacral floorplates on the oral surface (Figure 5.13) (Sumrall, 1992; Sumrall and Parsley, 2003). This allowed rapid contraction of the theca in response to stress or predators. The anal pyramid covers opened, spewing forth a stream of water as the theca collapsed (Sumrall, 1992).

The similarities between the ambulacral floorplate projections of this taxon and those of the discocystinids suggest that the projections functioned identically in both groups. While *Stromatocystites walcotti* lacks an aboral pedunculate zone, the aboral surface is broad and flat, and is bordered by a peripheral rim, resulting in an overall concave shape. Instead of using ligaments to contract the theca as in the discocystinids, *S. walcotti* used the ligaments to depress the aboral surface. The peripheral rim remained in contact with the substrate, inducing a tight seal as the aboral surface was raised.

The inner surface of the aboral surface is unknown, but it can be assumed attachment processes or rugosity indicative of ligamental attachment could be found.

The centrodorsal plate is immediately opposite the oral frame, which bears no projections, and therefore has no ligamental attachment to the aboral surface.

The presence of two different sizes of *Stromatocystites* is explained as an ontogenetic difference, an explanation first posited by Termier and Termier (1969). The problem with this interpretation is the occurrence of different sizes of the animal occurring in different beds. Juveniles do seem to be gregarious (Figure 5.14), suggesting that these may represent an echinodermal "nursery." Juveniles it appears were small enough to be capable of attaching to trilobite debris; one type specimen may be attached to the free cheek of an *Olenellus thompsoni* trilobite (Figure 5.14). Adults however grew to be much larger, with widths up to 37 mm, which excludes trilobite cephalons as appropriate substrates. The most likely substrate surface would have been algal matgrounds or possibly rocky nearshore areas. If the latter was the case, the animals may have been swept away by storms and buried in lower energy offshore environments, along with coarser sediment. *Stromatocystites* is similar both in its low profile and suction attachment to polyplacophorans, monoplacophorans, and some archaeogastropods, which also attach to hard substrates in high-energy environments. A sedimentological study of the rock in which *Stromatocystites walcotti* is required to satisfy this issue; algal binding similar to that seen in the studies of helicoplacoids carried out by Dornbos and Bottjer (2000, 2001) would indicate autochthonous preservation, while intervals of coarser sediment suspended by storms entombing the remains of large adult fossils would indicate allochthonous preservation.

The low profile of the test indicates that *Stromatocystites walcotti* was a low-level suspension feeder, another line of evidence for allochthonous preservation; an essentially

planar aboral surface would not be as efficient in lower-energy environments, as it does not extend any distance away from stagnant bottom waters.

Growth

The Extraxial-Axial Theory (Mooi et al., 1994; Mooi and David, 1997; 1998) and subsequent work on growth of stalked echinoderms from Sprinkle and Guensburg (2001) provide a framework for discussing the growth of the skeleton of *Stromatocystites walcotti*. Each skeletal region experienced growth in concert with the other skeletal regions.

The axial region consists of the oral frame and ambulacral areas. The ambulacra are composed of biserially arrange plates that are larger toward the mouth, and smaller toward the peripheral rim. This indicates that these elements are inserted at the ambitus according to the ocular plate rule of Mooi and David (1998), and continue to grow in size during the life of the animal. As in *Camptostroma*, the growth of the adjacent interambulacral areas was necessarily coordinated with the ambulacra as a different growth rate in either would cause shear between these skeletal regions as the animal grew. Furthermore, the ambulacral floorplates and the adjacent interambulacra show interdigitating lateral projections, which is further evidence that shear between these skeletal regions was impossible.

The perforate extraxial region constitutes the interambulacra of the oral surface. These plates as well as the ambulacra are larger toward the mouth, and smaller toward the edge of the oral surface, which indicates that these areas grew by plate insertion at the edge of the area, and subsequent growth of inserted plates. Also as in *Camptostroma*,

increase in width of the interambulacra was accommodated for by an exponential increase in the rate of plate insertion, as increasingly smaller plates accounted for increasingly more surface area. At the distal edge of the interambulacral areas are zones of small isotropic plates, which mark the edge of the oral surface, the transition to the imperforate extraxial region, and the peripheral rim.

The imperforate extraxial region is also marked by large plates centrally, and smaller peripheral plates. The centrodorsal plate represents the primordial aboral plate, fringed by a number of large elongate polygonal plates. Aboral plates are inserted at the peripheral rim, and grow during life. The growth is necessarily coordinated with the overlying ambulacral floorplates, with which the aboral surface shares a ligamental connection.

There are then two zones of plate insertion in *Stromatocystites walcotti*, as opposed to the four in the edrioasteroid *Camptostroma roddyi*; the terminals at the ambulacral tip, which adds plates of the axial region, and the peripheral rim, which acts as a zone of plate insertion for both the perforate and imperforate extraxial regions.

Systematic Position

It has become clear through the study of this edrioasteroid that it does not belong in genus *Stromatocystites*. The aboral surface differs dramatically from that of *S. pentangularis* and *S. reduncus*, and shows dramatically different ambulacral floorplates (Smith, 1990; Guensburg and Sprinkle, 1994). Both of these characters suggest different modes of attachment, and probably different substrates. While *S. walcotti* apparently attached to large patches of hard substrate by elevating the entire aboral surface while the

peripheral rim remained in contact with the substrate. *Stromatocystites pentangularis* and *Stromatocystites reduncus* were capable of attaching to smaller patches of substrate by constricting radial muscles, which in turn puckered a small raised pentangular pad on the aboral surface (Smith and Jell, 1990).

Smith and Jell (1990) and Guensburg and Sprinkle (1994) noticed "isorophid synapomorphies" expressed in the ambulacra. These included a trough shape to the food groove, and a lack of sutural pores in the ambulacral floorplates. I disagree with the latter interpretation; there is a clear space between laterally adjacent ambulacral floorplates through which ampullae could pass. Nonetheless, as previously discussed, the projections of the floorplates are similar to those of discocystinid isorophids. It is possible that *S. Walcotti* represents an ancestral isorophid; this would require development of a pedunculate zone between the aboral and oral surfaces. This trait may be convergently adapted in other groups, and therefore difficult to trace within the group, as a zone exists between the aboral attachment surface and oral surfaces of *Camptostroma* as well. For the time being, it is prudent to leave the taxon within the family Stromatocystitidae.

SYSTEMATIC PALEONTOLOGY

PHYLUM ECHINODERMATA de Bruguière, 1791

CLASS EDRIOASTEROIDEA Billings, 1858

ORDER STROMATOCYSTOIDA Termier and Termier, 1969

FAMILY STROMATOCYSTITDAE Bassler, 1936

Family Agelacrinidae Bather, 1900

Family Agelacrinitidae, Bassler, 1935

GENUS *SCHUCHERTIDISCUS nov. gen.*

Diagnosis – Theca has overall flattened profile; aboral surface lacks relief and shows a medial centrodorsal plate. Each ambulacral floorplate has a pair of elongate lateral projections oriented perpendicular to the direction of the food groove.

Description – Discoidal edrioasteroid with a robust peripheral rim composed of large flat plates, and a profile that kept the animal close to the surface of the substrate to which it attached. Five long straight ambulacra radiate in a "2-1-2" pattern from a mouth located at the center of the oral surface, which faced upward in life. Ambulacral tips are locked into edge of the peripheral rim. Oral frame is composed of 11 plates, one of which is disproportionately elongate, and is interpreted as being associated with the hydropore (Smith, 1985).

Discussion – The characters mentioned in the generic diagnosis are unique to the taxon, and are found in neither *Stromatocystites pentangularis* nor *Stromatocystites reduncus*, justifying the assignment of this taxon to a new genus. In particular, the aboral surface of *Stromatocystites* shows a pentagonal pad in high relief relative to the

remainder of the aboral surface, with a raised edge, which it used to attach to substrates. *Schuchertidiscus* on the other hand utilized the entire aboral surface for attachment, using the peripheral rim to induce a tight seal (Figure 5.11). There is no similar relief on the aboral surface; the only aboral relief is associated with the peripheral rim.

The low profile of the animal suggests that they were attached to hard substrates in a higher energy environment than that of other Early Cambrian echinoderms, and may have been loosened by storms and carried to lower energy environments and preserved along with coarser sandstones within mudstones. A lower profile would be advantageous in higher energy environments to minimize drag, while other echinoderms on lower energy environments extend some distance into the water column, via thecal elongation or development of brachioles.

While the lateral finger-like projections from the bases of the ambulacral floorplates are suggestive of similar projections in the isorophid edrioasteroids, *Schuchertidiscus* does not show any other isorophid synapomorphies, which suggests that these are convergently derived structures. The author does not discount that this possible isorophid ancestral relationship may be upheld out by a more inclusive taxonomic study of the Edrioasteroidea, as in Guensburg and Sprinkle (1994) and Smith and Jell (1990), but because of the focus of this study, cannot be borne out here.

Etymology – Named in honor of the collector and author of the original description, Charles Schuchert (Schuchert, 1919).

SCHUCHERTIDISCUS WALCOTTI Schuchert, 1919

Stromatocystites walcotti Schuchert, 1919, pg. 1-7, fig. 1a-d, plate 1 fig. 1-4; Termier and Termier, 1969, pg. 134-137, fig. 4; Paul and Smith, 1984, pg. 452-455, fig. 6-7; Smith, 1985, pg. 740-744; fig. 4, 7, 16, plate 88; Guensburg and Sprinkle, 1994, fig. 3.

Type material – Holotype, UCMP 66443.

Diagnosis – Anal pyramid in the CD interray, located away from midline toward the D ambulacrum. Interambulacral plates are large and polygonal, and show epispires along the edges. Adults grow to a diameter of 37 mm in width.

Description – Ambulacra show a great deal of relief. Epispire-bearing interambulacral plates are larger toward the mouth and smaller toward the edge of the oral surface; overall the interambulacral plates are lager than those of *Stromatocystites*. Aboral surface is composed of tightly sutured polygonal plates, which are also larger toward the mouth.

Discussion – The interambulacral plates of *Schuchertidiscus* are much larger than those of *Stromatocystites*; it was suggested by Schuchert (1919) that up to 130 interambulacral plates made up the oral surface of *Schuchertidiscus*, while as many as 1,000 comprise the oral surface of *Stromatocystites*.

Juvenile specimens of this taxon were diagnosed by Schuchert (1919) as a different sub-specific group; Termier and Termier (1969) recognized these were merely juveniles. The author agrees with this assessment, but aside from a robust peripheral rim, these juveniles do not show any of the emergent traits of the group. Furthermore, no stratigraphic information exists for either the adults or juveniles, which is complicated by

the fact that Schuchert (1919) noted that each came from separate beds, despite not mentioning which group of specimens came from which bed, or leaving similar notation with the type specimens. While it is possible that these represent different species, it is parsimonious at this point to assume that the smaller echinoderms are juveniles of the adult form. Further collection of the type locality is called for in order to resolve this issue. As is the case in any taxon known from few specimens, further collection is always called for, and would also be helpful in understanding the external aboral surface, especially the ambulacral coverplate series, and hydropore position.

Etymology – Named in honor of Charles Doolittle Walcott, Secretary of the Smithsonian Institution at the time of initial publication (Schuchert, 1919).

Occurrence – Early Cambrian *Bonnia-Olenellus* Zone of Bonne Bay, western Newfoundland, Province of Newfoundland and Labrador, Canada.

Conclusions

1. *Schuchertidiscus walcotti* represents a new genus, distinct from the Middle Cambrian edrioasteroid *Stromatocystites*.

2. *Schuchertidiscus* attached to large patches of hard substrate, using the peripheral rim to induce a seal. Suction was accomplished by elevation of the aboral surface by ligaments attached to finger-like projections extending from the bases of ambulacral floorplates.

3. Traits unique to the group include a flat aboral surface with a centrodorsal plate, and a pair of projections on the base of the ambulacral floor plates. These traits are not found

in other groups, including *Stromatocystites*, with which it is likely related but clearly differentiated from.

Figure 5.1. Bonne Bay (B) Newfoundland, Province of Newfoundland and Labrador, Canada.

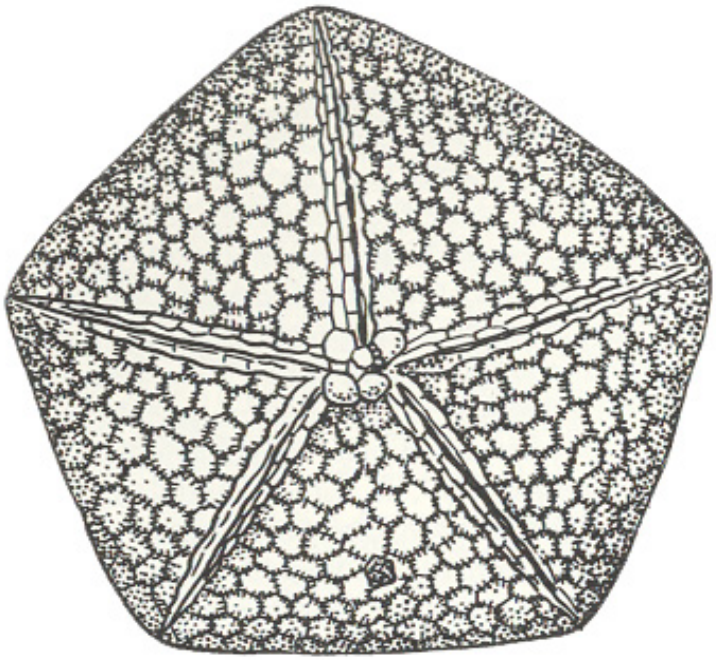


Figure 5.2. *Stromatocystites pentangularis* Pompeckj, 1896.

Figure 5.3. "*Stromatocystites walcotti* minor" Schuchert, 1919. Aboral surface; metric ruler for scale.

Figure 5.4. *Schuchertidiscus walcotti* Schuchert, 1919. USNM 66443; metric ruler for scale.

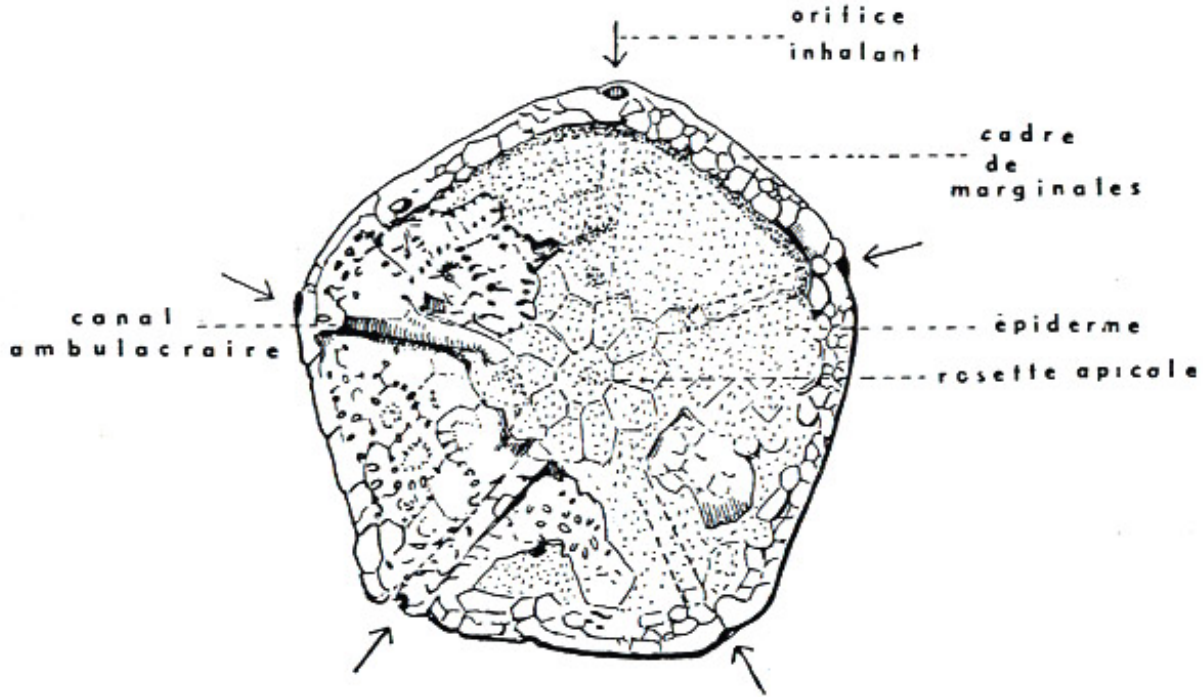


Figure 5.5. Termier and Termier (1969) Reconstruction of "*Stromatocystites" walcotti* Schuchert, 1919. Reconstruction is based on USNM 376690 (Figure 4). Arrows indicate inhalant orifices.

Figure 5.6. *Stromatocystites pentangularis* Pompeckj, 1896, top. *Stromatocystites reduncus* Smith and Jell, 1990. Both in external aboral view. Both species show a distinct pentagonal medial pad. Metric ruler for scale.

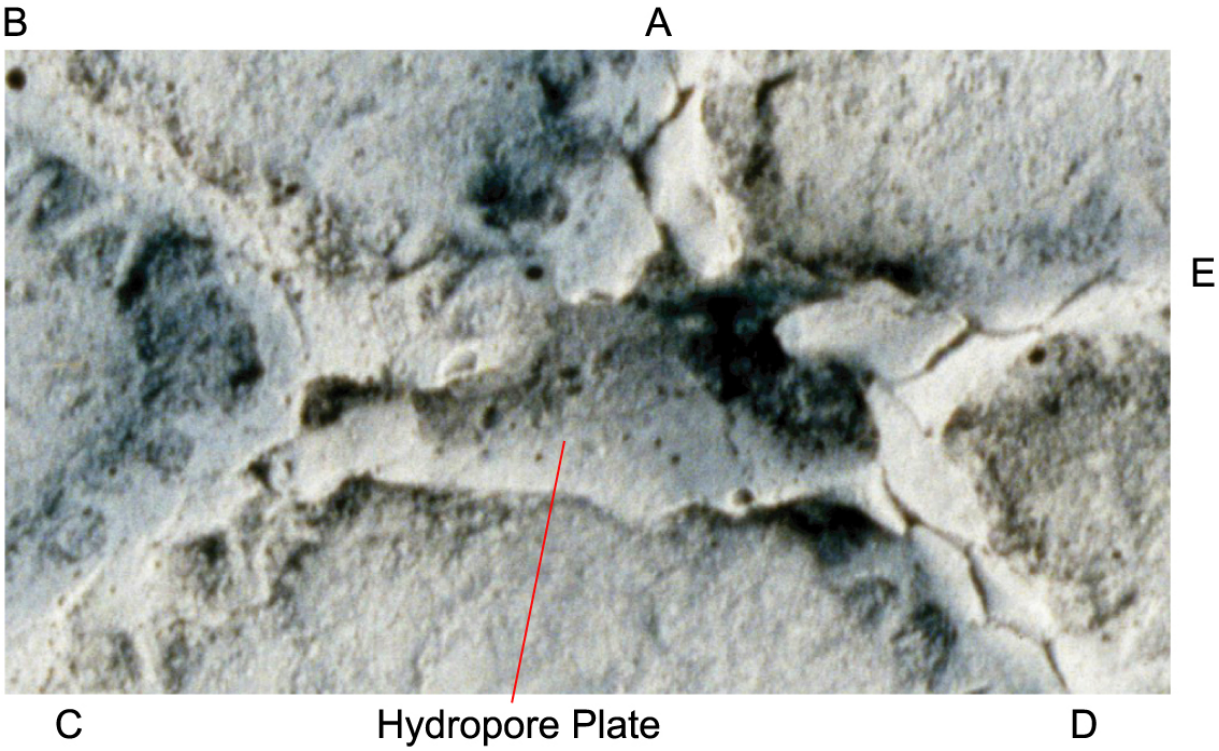


Figure 5.7. Oral frame, internal view, USNM 376690. Ambulacra are labeled according to the Carpenter System of notation (Carpenter, 1884). Field of view is 21 mm wide.

Figure 5.8. D Ambulacrum, USNM 376690, mouth is toward the left. Note biserial arrangement and decreasing size away from moth. Ambulacrum is 16 mm long.

Figure 5.9. Interambulacral plate ornament in juvenile specimen. Field of view is 7 mm across.

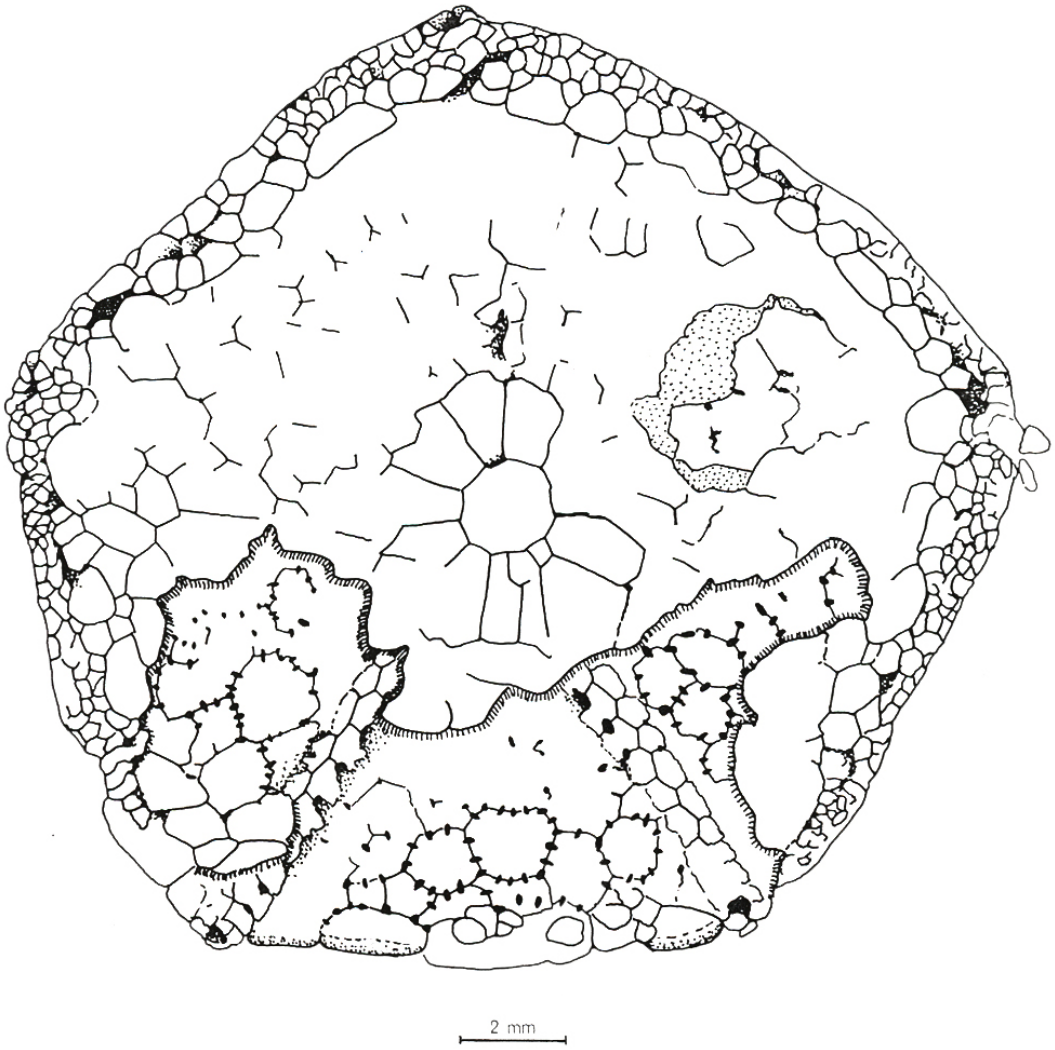


Figure 5.10. *Schuchertidiscus walcotti* Schuchert, 1919, aboral surface. Centrodorsal plate lies medially; lower portion of aboral surface has been removed by taphonomic processes, revealing the interior of the oral surface. Drawing is from Smith, 1985.

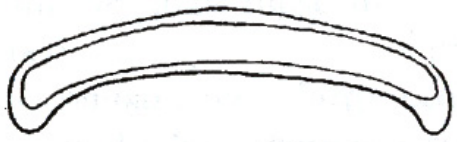


Figure 5.11. Cross-sectional profile of *Schuchertidiscus walcotti* Schuchert, 1919. Oral surface is facing up. From Schuchert, 1919.

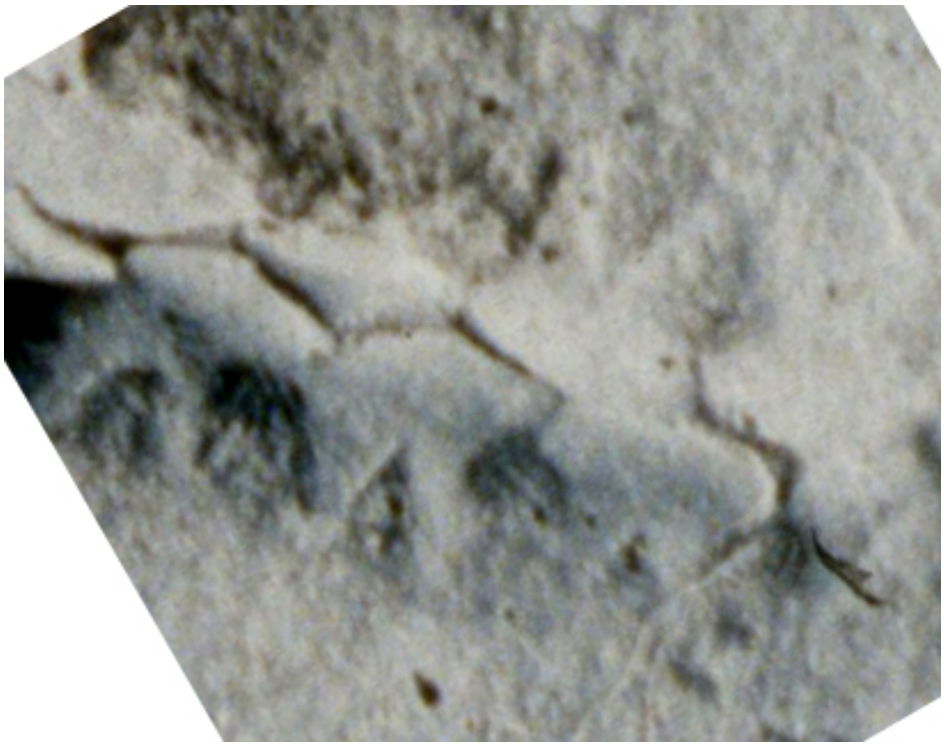


Figure 5.12. Detail of D ambulacrum. Note pairs of projections perpendicular to the trend of the ambulacral groove. Field of view is 5 mm across.

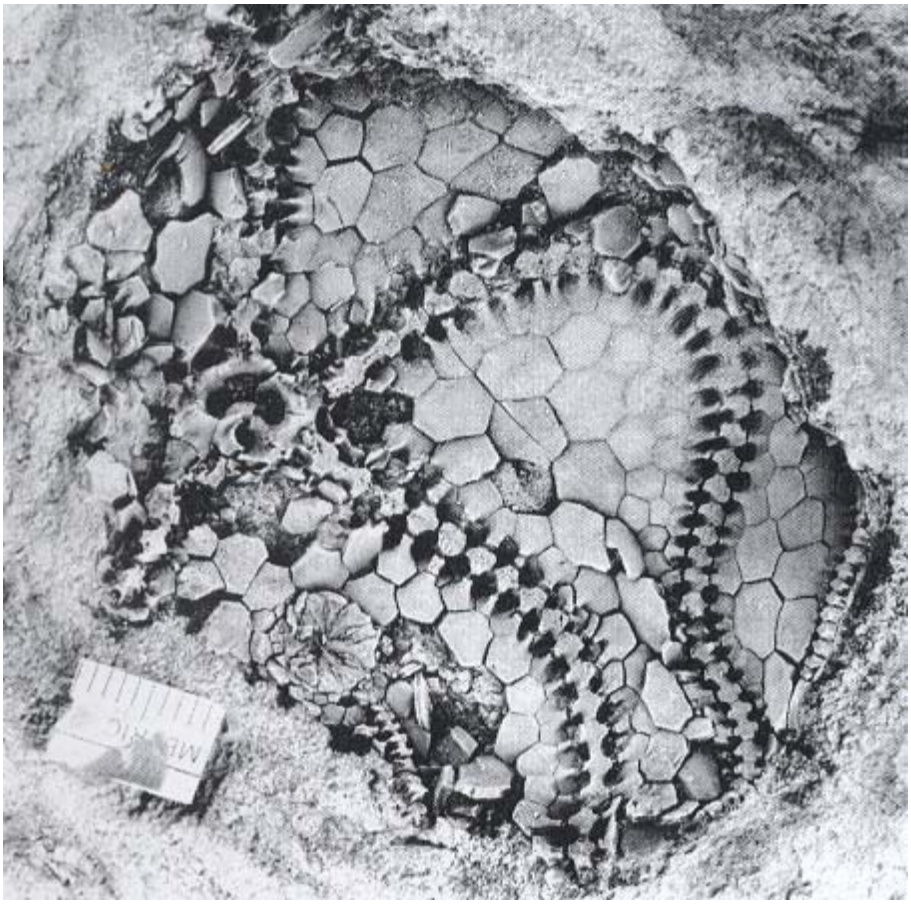


Figure 5.13. *Hypsiclavus huntsvillensis* Sumrall, 1996, interior view of oral area. Note lateral projections at the bases of the ambulacral floorplates. Specimen is 6.4 mm across. Figure taken from Sumrall and Parsley, 2003.

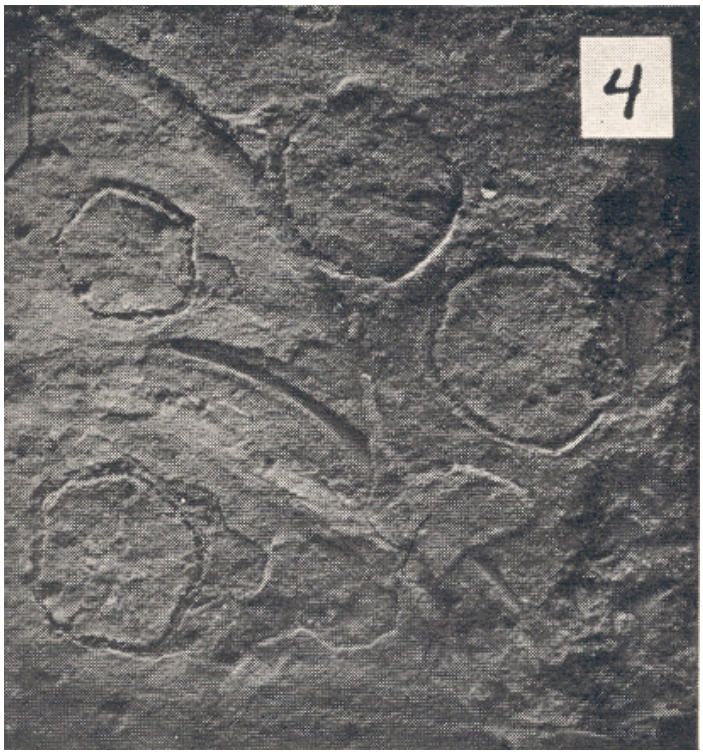


Figure 5.14. *Schuchertidiscus walcotti* Schuchert, 1919. Juvenile specimens; specimen is upper left may be attached to *Olenellus* trilobite fragment. Photograph from Schuchert, 1919 (Plate 1, figure 4). Field of view is approximately 50 mm across.

Chapter 6 – Early Cambrian Echinoderm Systematics

Introduction

Many investigators of the early radiation of echinoderms and general trends in echinoderm morphology have included rudimentary non-computational trees with their studies. There has been no tree yet that has included all Early Cambrian taxa. Considering the stratigraphic position of these earliest members of so successful a group, and the additional taxa described and revisions carried out here, a new analysis of Early Cambrian echinoderms and crown taxa is warranted.

Past Investigations

Paul and Smith (1984) included a tree in their discussion of the radiation and phylogeny of echinoderms (Figure 6.1). The authors scored 20 characters for 10 taxa; including the Early Cambrian groups revised here, representative fossil taxa and the five echinoderm crown groups (Crinozoa, Holothuria, Echinoidea, Ophiuroidea, and Asteroidea) to non-computationally generate a tree that spans the Phanerozoic. Helicoplacoids and carpoids were considered outgroups, under the premise that pentamery is derived. *Camptostroma*, *Stromatocystites*, and the pelmatozoans form a polytomy. *Gogia* and *Kinzercystis* form a clade, as do *Lepidocystis* and *Echmatocrinus*, which is proposed to be the ancestor of the crinozoa. This arrangement makes the Imbricata [*Kinzercystis + Lepidocystis*] a polyphyletic group.

Smith (1985) followed this work with a phylogeny of the edrioasteroids in the Cambrian (Figure 6.2). Smith omitted *Camptostroma* from this study, and generated a

phylogenetic tree with *Stromatocystites* as the outgroup, based on a matrix of 13 taxa and 22 characters. The outgroup was scored by analyzing characters from both *Stromatocystites reduncus* and *Shuchertidiscus walcotti*. As in the Paul and Smith 1984 paper, the tree generated in this study was non-computational.

A second study conducted by Smith (1988) focused on the relationships of four Early Cambrian taxa; *Helicoplacus*, *Camptostroma*, *Lepidocystis*, and *Stromatocystites*. Smith used non-computational methods to compare nine polarized characters considered taxonomically important. The polarization is based on the premise that *Helicoplacus* is basal based on triradiate ambulacra and lack of epispires. The taxon used to score characters for the Early Cambrian taxon "*Stromatocystites"* is again the Middle Cambrian taxon *Stromatocystites reduncus*, and not the taxon redescribed here as *Shuchertidiscus walcotti*. The tree shows *Helicoplacus* as the most basal member based on the triradiate ambulacra, while *Camptostroma, Stromatocystites*, and *Lepidocystis* form a monophyletic group. These results show that the group Edrioasteroidea (as presently understood) is paraphyletic, as the lowest node that includes all edrioasteroids also includes the eocrinoid *Lepidocystis* (Figure 6.3).

Although no phylogenetic tree was created for the helicoplacoids in Durham and Caster (1963, 1966), and Durham (1964, 1967, 1993), relationships can be assessed through traditional Linnean taxonomy (Table 6.1). These designations were made by comparison of characters as discussed by Durham (1997) and revisited in the chapter here on the topic of helicoplacoids. The taxa *Helicoplacus* and *Westgardella* have been synonymized, leaving *Helicoplacus gilberti*, *Polyplacus kilmeri*, and *Waucobella nelsoni* as the only valid species from this list.

Sumrall (1997) created a phylogeny for all echinoderms, including the Early Cambrian groups *Camptostroma*, the helicoplacoids, Imbricata (lepidocystids), and *Gogia*. Trees were generated by employing a heuristic search in the computer program PAUP (Swofford, 1992). Unlike the other trees, Sumrall used *Camptostroma*, *Helicoplacus*, and *Lepidocystis* as outgroups to polarize characters (Figure 6.4). The Edrioasterid edrioasteroids lay crownward, as does *Gogia*, which along with the Crinozoa, lie within the monophyletic group Blastozoa. Notable departures from standard echinoderm interpretations are that the lepidocystids are not eocrinoids, while crinoids are.

David et al. (2000) generated a tree for a paper on the phylogenetic position of homalozoans using non-computational methods. The authors generated a topology, and added characters in support of each branch. A polytomy at the base of the tree showed an unresolved node between helicoplacoids, edrioasteroids, and the remainder of all skeletized echinoderms. *Arkarua adami* (Gehling, 1987) was used as the outgroup, but is not necessarily an echinoderm, as the only echinoderm character it shows is pentamery, which is homoplasic across the metazoa. While the purpose of this tree was not to elucidate basal relationships, it did show that the authors considered edrioasteroids to be a monophyletic group (Figure 6.5).

This study

A new phylogeny was generated for the Early Cambrian taxa included in this study, as well as crown echinoderms, and homalozoan echinoderms. These include *Trochocystites bohemicus* Barrande, 1887 (Ubaghs, 1968c), *Castericystis sprinklei*

Ubaghs and Robison, 1988, *Ctenocystis utahensis* Robison and Sprinkle, 1969, and *Cothurnocystis bifida* Ubaghs and Robison, 1988. These are all Middle Cambrian taxa, and represent the first homalozoans in the record.

. A matrix of 20 characters was generated with MacClade 4.06 (Maddison and Maddison, 2003), and data analysis was carried out in PAUP 4.0b10 (Swofford, 2002).

Characters

A character is a heritable and observable part of an organism (Sumrall, 1996; Wiley et al. 1991). Useful characters for taxonomic studies are discrete, which makes assignment of character states possible. Characters that vary are given a score according to the character state: "0" or a "1" for binary characters, with higher numbers assigned in the case of multi-state characters. If the character state cannot be scored based on the material available, it is scored with a question mark (for example characters associated with the ambulacral cover plates of *Shuchertidiscus* cannot be scored, as the animal is only known in aboral view), whereas if the character is not applicable for a particular taxon, a dash is used (for example a character pertaining to holdfasts for an asteroid).

In regard to character polarity, "0" is generally reserved for plesiomorphic characters, and "1" for derived. Without a Precambrian record of echinoderms, character polarization proves difficult. Some analyses use stratigraphy as a proxy for polarizing characters; Early Cambrian echinoderms are too disparate with too little time separating groups to safely employ this method of character polarization. For this reason, the tree generated in this study is unrooted. Possible polarization techniques will be discussed further in the discussion section.

Character choice is vital in this study, as previous workers have used characters that change over the life span of the organism to delineate taxonomic groups (Durham, 1967, 1993). The result was a comparison of differing ontogenetic groups, rather than differing taxonomic groups. In particular, helicoplacoid interambulacral ridge plates show grooves along the edges early in ontogeny, and loose them later in life. Sampling of fossil taxa in this regard is imperative, as factors associated with growth and sexual dimorphism can be ruled out as taxonomically important characters by study of a wealth of specimens

The 17 taxa were scored for these twenty characters, which account for 54 possible character states.

Character Description

1. Epispires present (0), present with epispire cover plates (1), or epispires absent (2).

Epispires are respiratory passageways along plate sutures in the perforate extraxial region. Most of the taxa included show epispires, with the exception of the helicoplacoids, most homalozoans, and crown echinoderms. *Camptostroma roddyi* shows epispires with lath-shaped cover plates.

2. Five (0), three (1), two (2), or zero (3) ambulacra.

A synapomorphy of the Echinodermata is pentameral symmetry, or some variant thereof. Helicoplacoids are an exception, with three, while *Trochocystites* shows two, and the remainder of the "carpoid" groups show no ambulacra at all.

3. Ambulacra are curved distally (0) or straight (1).

Helicoplacoids and *Camptostroma roddyi* show ambulacra that are curved at the distal tips, while the remainder echinoderms in this study show straight ambulacra.

4. Brachioles absent (0), present and straight (1), present and spiraled (2), or some other coverplate-bearing erect feeding appendage (3).

Gogia and the lepidocystids have brachioles, which are erect feeding appendages that branch from the ambulacra. They are either spiraled, as in the case of *Gogia*, or straight, as in the case of the lepidocystids. Some of the carpoid groups share the character of an erect feeding appendage, with cover plates. While not necessarily a brachiole, it is an additional type of erect feeding appendage, and is scored accordingly.

5. Imperforate extraxial region comprises approximately half of the theca (0), a majority of the theca (1), or is greatly reduced (2).

The imperforate extraxial region comprises the aboral half of *Camptostroma*, *Shuchertidiscus*, and *Gogia*. It comprises the majority of the test in the helicoplacoids and lepidocystids, and is greatly reduced in the "carpoid" groups and crown taxa.

6. Imperforate extraxial region arranged into a broad pad (0), a constricted pad with flanking pleats (1), a pad with adjacent imbricate plating (2), a pad with adjacent polygonal plating (3), or reduced (4).

The imperforate extraxial region is organized into a large flat pad for attachment, as in *Shuchertidiscus*, or flanked by pleats, as in the helicoplacoids and *Camptostroma*, or

flanked by imbricate plates as in the lepidocystids, or reduced to the point at which it no longer serves to function as a pad.

7. Theca domal (0), bulb-shaped (1), conical (2), globular (3), or laterally compressed (4).

Camptostroma and *Shuchertidiscus* show a domed theca, while helicoplacoids show a bulb-shaped theca. Some of the eocrinoids have an inverted-conical shape, and others are globular. Some crown echinoderms and the homalozoans are laterally compressed.

8. Ambulacra covering comprised of two rows of cover plates (0), three or more rows of cover plates (1), or are absent (2).

Ambulacral cover plates are arranged into two rows, as in *Helicoplacus gilberti* and *Waucobella nelsoni*, or by three or more rows of cover plates, as in *Waucobella nelsoni* and *Camptostroma roddyi*. This character cannot be scored in other Early Cambrian groups as it is not preserved in any other fossils, while other taxa have lost the coverplates altogether.

9. Secondary cover plate to primary cover ratio is 2:1 (0), or 3:1 ratio (1).

The secondary cover plates lie above the primary cover plates. In *Trochocystites bohemicus*, *Helicoplacus gilberti* and *Polyplacus kilmeri* there are two secondary cover plates for every primary cover plate; in *Camptostroma roddyi* and *Waucobella nelsoni* there are three.

10. One (0) or two (1) brachiolar cover plates per brachiolar plate.

For those taxa that have brachioles, each brachiolar cover plate is roofed by a single cover plate, or two.

11. Aboral pad straight edged (0), ring-shaped (1), or flared (2).

For those organisms that have an aboral pad, the pad is the same width as the structure that it is attached to, as in the lepidocystids, helicoplacoids, *Gogia mccollumi*, *Shuchertidiscus*, and *Camptostroma*, or ring-shaped, as in *Gogia fowleri* and *Gogia inyoensis*, or flared, as in *Gogia ojenai* and *Gogia lockeri*.

12. Umbo upon thecal plates absent (0) or present (1).

Gogia fowleri and *Gogia inyoensis* show a small umbo. This structure is a raised conical projection in the middle of the thecal plates. No other echinoderms in this analysis show this structure.

13. Anal pyramid present (0) or absent (1).

The anus in most early echinoderms is roofed by a series of lath-shaped plates, that when retracted, form a cone- or pyramid-like structure over the anus. Many crown echinoderms and the helicoplacoids have lost this structure.

14. Rhombus-shaped plate at the junction of the ambulacral cover plates and floor plates absent (0) or present (1).

Waucobella nelsoni shows a unique rhombus shaped plate in the ambulacra. It is not seen in any other echinoderm groups. Taxa for which this character cannot be scored are designated with a "-" and taxa for which this character probably exists but cannot be scored based on the available material are designated with a question mark.

15. Theca is rigid (0) or flexible (1).

The theca of *Camptostroma*, *Ctenocystis*, and the helicoplacoids was flexible, allowing for some degree of shape and perhaps volumetric change. The remainder of the taxa show skeletal plates more tightly sutured, indicating rigidity of the test.

16. Stalk plating undifferentiated from thecal plating (0) or differentiated (1).

Different plating types differentiate the stalk in *Gogia* from the rest of the animal, while the stalk in the lepidocystids is identical to that which makes up the theca.

17. Recumbent ambulacra are long (0) or reduced in length (1).

The ambulacra in *Gogia* are reduced in size relative to the size of the animal, whereas the remainder of the groups shows ambulacra that extend for some distance over the theca.

18. Stalk absent (0) or present (1).

The lepidocystids and *Gogia* have a stalk, which served to elevate the theca from the substrate.

19. Additional non-feeding appendage absent (0) or present (1).

The homalozoan groups show an additional appendage that was not used in feeding, as shown by the lack of cover plates, or attachment, as shown by the lack of distal attachment pad.

20. Attached (0) or free-living (1).

The Early Cambrian echinoderm groups included in this analysis all lived attached, as deduced by morphology (attachment pad) or by direct observation (specimens attached to skeletal debris). The crown taxa and "carpoid" echinoderms were free-living, as shown by a lack of attachment structures.

Discussion

The computer program Paup 4.0b10 (Swofford, 2002) was used to carry out a phylogenetic analysis for this data (Table 6.2). Carrying out a heuristic search, with the parsimony optimality criterion, using 100 replications with the tree-bisection-reconnection branch-swapping algorithm, generated a single most-parsimonious tree (Figure 6.6). The tree length (TL) is 39 steps, consistency index (CI) is 0.872, and the retention index (RI) is 0.935. The high consistency index shows that there is very little homoplasy in the generated tree, and the high retention index shows that there is very little apparent homoplasy.

A Bootstrap 50% majority rule consensus tree was also generated (Figure 6.7). Resampling of the data was replicated 100 times, and compared to the original tree

topology. All branches were recovered a majority of the time, with varying degrees of support. The least well-supported branch is for the clade that includes *Helicoplacus gilberti* and *Polyplacus kilmeri*. This is probably because of the paucity of scorable characters for *Polyplacus kilmeri*, which is essentially built entirely of ambulacra, making non-ambulacral characters unavailable for teasing out relationships within the helicoplacoids.

The tree topology shows support for many traditionally defined clades. *Gogia*, the lepidocystids, and Eocrinoidea [*Gogia* + lepidocystids] all comprise monophyletic groups. Contrary to the analyses of David et al. (2000) but in accord with Sumrall (1997), the homalozoans form a clade. Crown echinoderms form a sister group to the homalozoans. This is most probably because of the vagile nature of these groups, and the resultant morphology that lifestyle generates. Sister to this group is the clade that includes Eocrinoidea and *Shuchertidiscus*. The branch supporting this clade is not particularly well supported.

The traditionally defined group Edrioasteroidea contains the taxa *Shuchertidiscus* and *Camptostroma*. However, this group is not recovered in the analysis; rather Edrioasteroidea is polyphyletic. Edrioasteroids show a suite of simpler characters, and are rather generalized in body plan, rather than highly modified. Because of this, edrioasteroids have been proposed to be basal on the echinoderm tree (Paul and Smith, 1984; Smith, 1988; Guensburg and Sprinkle, 1994; Sprinkle and Wilbur, 2005). If this were the case, it is likely then that edrioasteroids are closer to a hypothetical ancestral echinoderm than any other taxa, and served as a template for the array of echinodermal body plans early in the Paleozoic. "Edrioasteroidea" is then a plausible name for a node

at the base of the echinoderm tree that resolves all echinoderms, rather than an inclusive group of stem taxa.

Although characters were not polarized in this study, based on the placement of Edrioasteroidea and general unelaborated characters associated with the group, it can be presumed that most of the characters associated with *Camptostroma* are ancestral to the group. Imbedded in this polarization is the assumption that helicoplacoids are derived, and that the triradiate ambulacra is not ancestral in echinoderms. It has already been argued in the preceding chapter on helicoplacoids and in Derstler (1982), and Sprinkle and Wilbur (2005) that the unique helical arrangement of the test and disassociation of the mouth and axis of symmetry are likely to be derived, as it requires fewer steps and to evolutionarily transform a generalized edrioasteroid into a helicoplacoid, than turning a helicoplacoid into an edrioasteroid. Furthermore, the edrioasteroid body plan, with the addition of a stalk and brachioles, approximates the eocrinoid body plan (Derstler, 1985).

According to the tree generated in this study, crown echinoderms must have existed during the Middle Cambrian or before, as they branch before the Middle Cambrian diversification of the Homalozoans. This lends credence to the premise made by Sprinkle (1973) that *Echmatocrinus brachiatus* from the Middle Cambrian Burgess Shale is a crinoid, and the questionable assignment made by Walcott (1911) of *Eldonia ludwigi* from the Middle Cambrian Burgess Shale to Holothuria. The position of the homalozoans within the echinoderm tree also supports the premise that these groups are echinoderms, and not "calcichordates," a group erected by Jeffries (1968) to include homalozoans as stem taxa of vertebrates. The brachioles, ambulacral cover plates, differentiation of the test into the three regions of the Extraxial-Axial Theory (Mooi and

David, 1997), and sister-taxon status with crown echinoderms all support the premise that these are echinoderms.

Conclusions

The monophyletic groups derived in this analysis include the eocrinoids, lepidocystids, *Gogia*, homalozoans, and the helicoplacoids. More importantly, the edrioasteroids are polyphyletic in this analysis. In order to redefine the group "Edrioasteroidea" as a monophyletic group, it is necessary to either exclude *Camptostroma roddyi*, or include all echinoderms as within-group taxa. This second option essentially means that all echinoderm taxa are edrioasteroids, a conclusion that is inescapable based on current definitions and the fossil record of echinoderms. The current definition of the group is uninformative, and necessitates redescription to reflect evolutionary relationships within the Echinodermata.

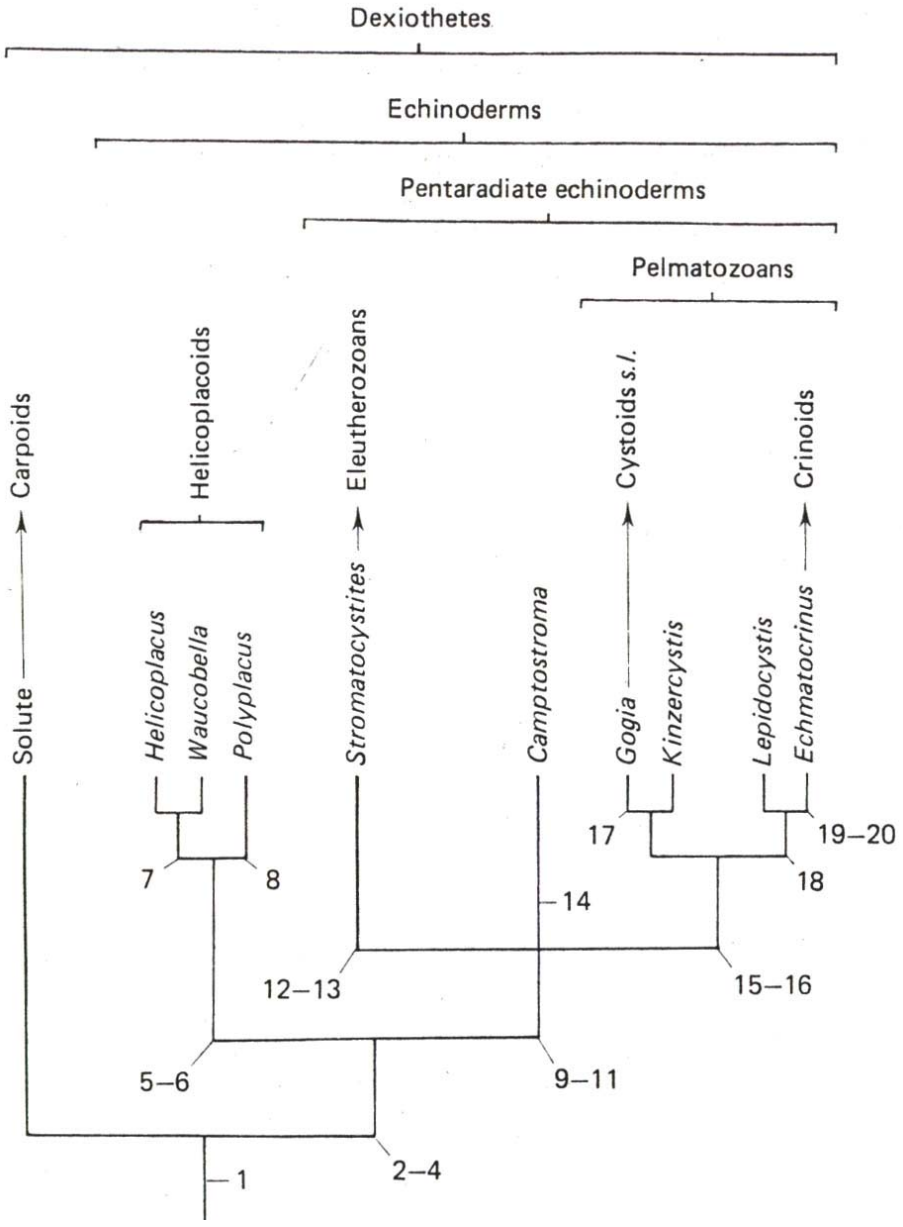


Figure 6.1. A suggested echinoderm phylogeny from Paul and Smith, 1984 (Figure 19, pg. 461).

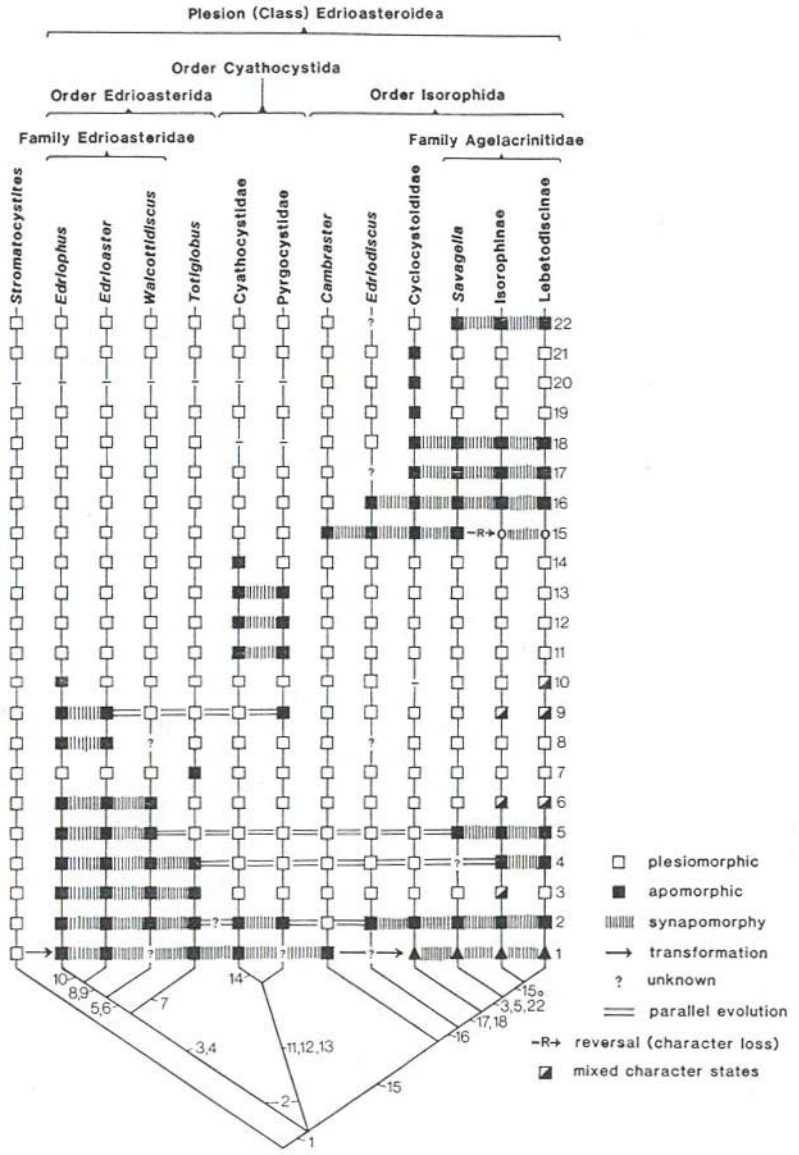


Figure 6.2. Cladogram and character list for Cambrian edrioasteroid taxa from Smith, 1985 (Text-Figure 12, pg. 735). Note the omission of *Camptostroma*.

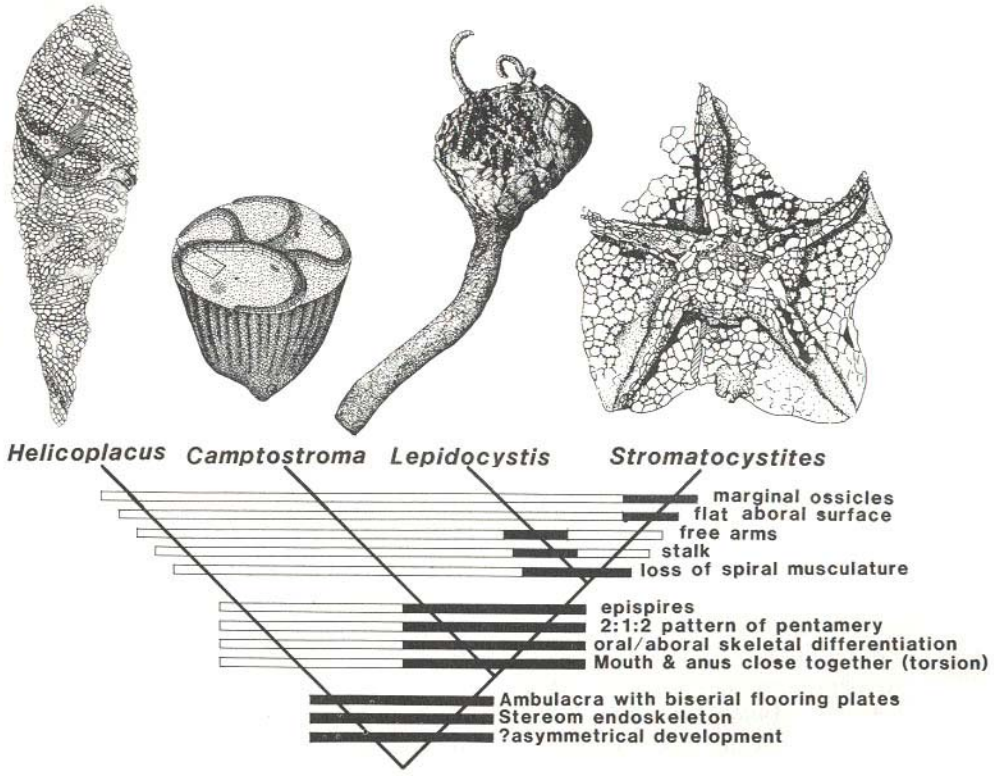


Figure 6.3. Cladogram and character list for four Early Cambrian echinoderms, from Smith, 1988 (Figure 7., pg 88). The "Lower" Cambrian drawing of *Stromatocystites* is based on *Stromatocystites pentangularis* from the Middle Cambrian.

Previous Workers:	
Class Helicoplacoidea	(Durham and Caster, 1963)
Subclass Helicoplacida	(Durham, 1967)
Family Helicoplacidae	(Durham and Caster, 1966)
Genus *Helicoplacus*	(Durham and Caster, 1963)
Helicoplacus gilberti	(Durham and Caster, 1963)
Helicoplacus everndeni	(Durham, 1967)
Helicoplacus casteri	(Durham, 1993)
Helicoplacus guthi	(Durham, 1993)
Family Westgardellidae	(Durham, 1993)
Genus *Westgardella*	(Durham, 1993)
Westgardella curtisi	(Durham, 1993)
Westgardella firbyi	(Durham, 1993)
Westgardella blancoensis	(Durham, 1993)
Genus *Waucobella*	(Durham, 1967)
Waucobella nelsoni	(Durham, 1967)
Subclass Polyplacida	(Durham, 1967)
Genus *Polyplacus*	(Durham, 1967)
Polyplacus kilmeri	(Durham, 1967)
This Study:	
Class Helicoplacoidea	(Durham and Caster, 1963)
Family Helicoplacidae	(Durham and Caster, 1966)
Genus *Helicoplacus*	(Durham and Caster, 1963)
Helicoplacus gilberti	(Durham and Caster, 1963)
Helicoplacus nelsoni	(Durham, 1967)

Table 6.1. Helicoplacoid systematics as suggested by the original authors.

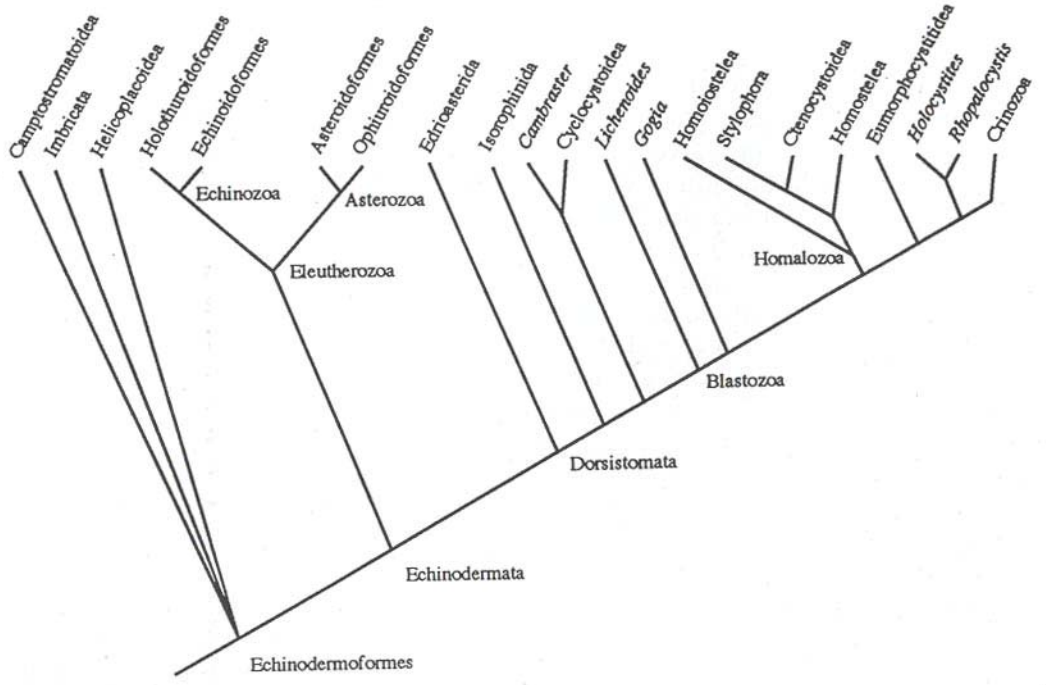


Figure 6.4. Echinoderm phylogeny, from Sumrall, 1997 (Figure 6, pg. 277). Note the polytomy between the basal-most taxa, and the position of *Gogia*.

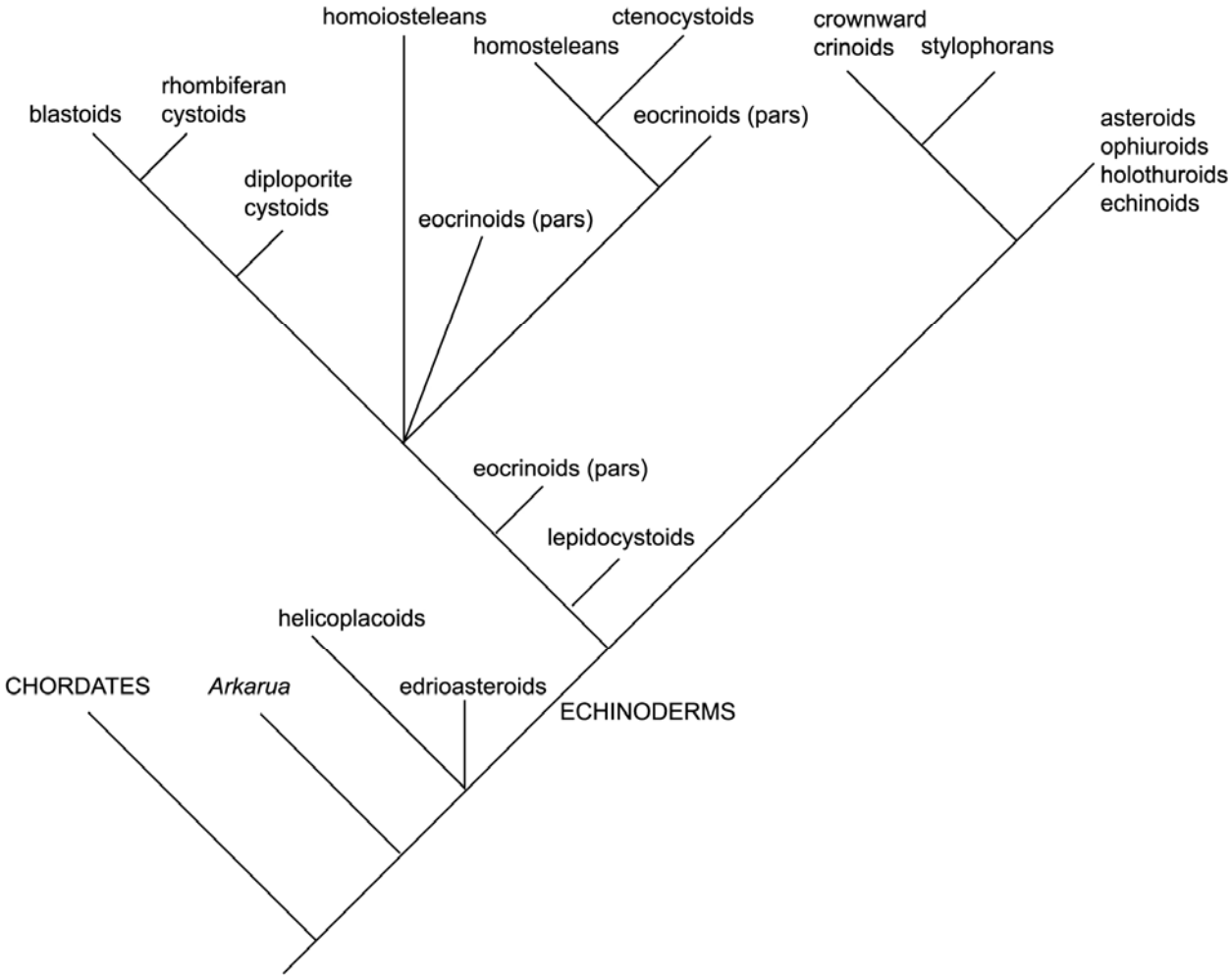


Figure 6.5. Echinoderm cladogram, redrawn from David et al., 2000 (Figure 9, pg. 549). Note the polytomy between helicoplacoids, edrioasteroids, and the variable possible positions of *Gogia*.

Taxon/Node	Character			
		1	11111	11112
	12345	67890	12345	67890
C. roddyi	10000	1010-	00001	-0000
S. walcotti	00100	00??-	00000	-0000
H. gilberti	21001	1100-	00101	-0000
W. nelsoni	21001	1111-	00111	-0000
G. ojenai	00120	33??1	200?0	11100
G. lockeri	00120	33??1	200?0	11100
G. fowleri	00120	33??0	110?0	11100
G. inyoensis	00120	33??0	110?0	11100
G. mccollumi	00120	32??0	000?0	11100
K. durhami	00111	22??0	000?0	00100
L. wanneri	00111	22??0	000?0	00100
P. kilmeri	21001	1100-	00101	-0000
Crown Echinoderms	20102	402--	-010-	-0001
Trochocystites	02132	042--	-0000	-0011
Cothurnocystis	23-32	042--	-00-0	-1011
Ctenocystis	23-02	042--	-00-1	-0001
Castericystis	23-32	042--	-00-0	-1011

Table 6.2. Character matrix for Early Cambrian taxa. Bold character numbers in the first row correspond to characters discussed in the text.

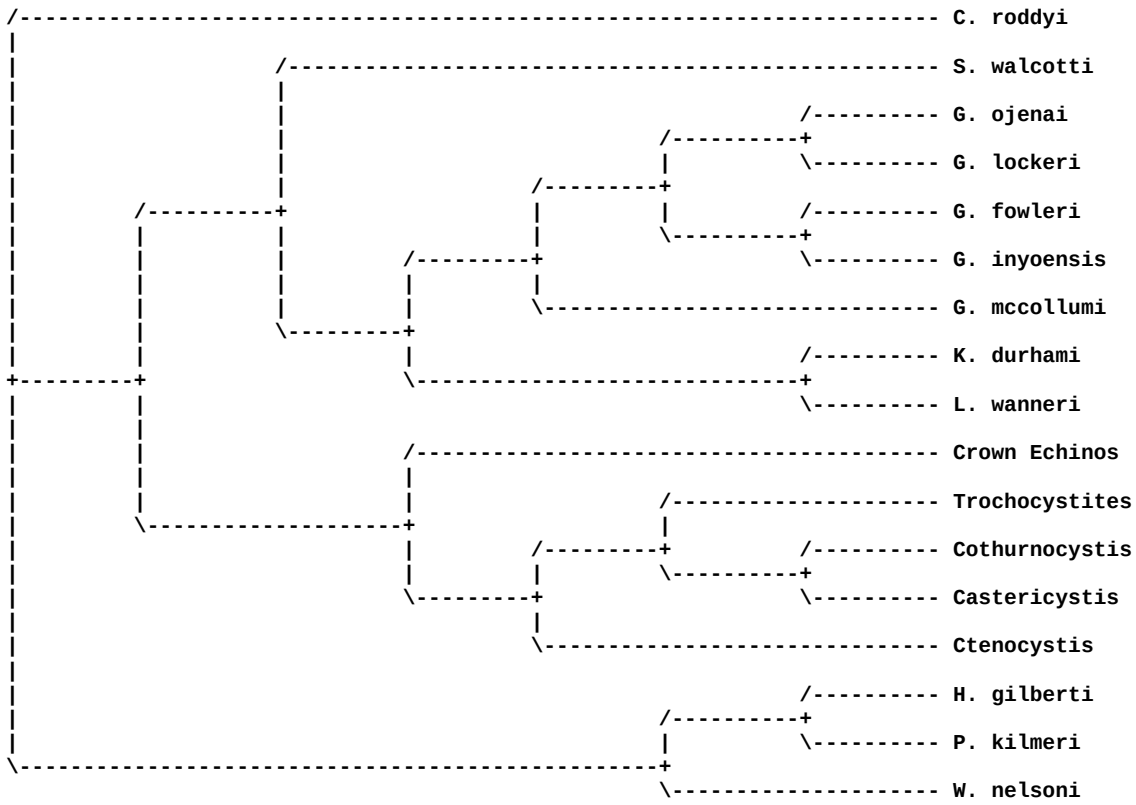


Figure 6.6. Most parsimonious tree recovered by heuristic search from the character matrix in Table 2.

Figure 6.7. Bootstrap 50% majority-rule consensus tree recovered from the character matrix in Table 2. Bootstrap support percentages for internal branches based on 100 replicates are shown.

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Vita

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